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New Amphicyonid Carnivorans (Mammalia, Daphoeninae) from the Early Miocene of Southeastern Wyoming

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New Amphicyonid Carnivorans (Mammalia, Daphoeninae) from the Early Miocene of Southeastern Wyoming

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ABSTRACT

Latest Arikareean sediments of the upper Arikaree Group in southeastern Wyoming produced rare fossils of large, early Miocene amphicyonid carnivorans for field parties of the Frick Laboratory, American Museum, from 1932 to 1940. Recent geologic field investigations, including mapping, have discovered additional remains of these carnivorans, clarifying their geographic and stratigraphic distribution, and permitting a more informed description of the earlier collections.

These carnivorans come from tuffaceous sandstones of the Upper Harrison beds, the terminal formation-rank unit of the Arikaree Group in southeastern Wyoming. A large species of the amphicyonid *Daphoenodon* (*D. falkenbachi*, n. sp.) occurs in northern Goshen and southeastern Platte Counties, Wyoming, and in the Niobrara Canyon, Sioux County, Nebraska. A smaller species of this genus (*D. skinneri*, n. sp.), probably ancestral to *D. falkenbachi*, is known from a single individual from southern Niobrara County, Wyoming. A third amphicyonid, *Adilophontes brachykolos*, n. gen., n. sp., is closely related to *Daphoenodon*, and is reported from northern Goshen County and east-central Platte County, Wyoming. The three species share a similar basicranial anatomy, including the form of the auditory bulla, and can be referred to the endemic North American amphicyonid subfamily Daphoeninae. They are found only in Upper Harrison strata in southeastern Wyoming and northwest Nebraska, and are presently unknown elsewhere in North America.

Postcranial remains indicate that these large predators lacked the extreme digitigrade specializations of the feet and limbs encountered in living canids and large felids. They are characterized by relatively short lower-limb segments, and paraxonic feet with slightly spreading digits, which might be termed subdigitigrade. These skeletal traits and their carnassiform dentitions with prominent canines, premolars, and shearing carnassials indicate a carnivorous diet probably obtained by a rapid rush from cover and a short, powerful pursuit of ungulate prey in open grassland and riparian stream settings east of the Rocky Mountain uplifts.

A new formal term, Anderson Ranch Formation, is proposed as a replacement for the Upper Harrison beds of Peterson (1909) that yielded the carnivores discussed in this study.

INTRODUCTION

Nonmarine tuffaceous sediments of the Arikaree Group blanketed much of southeastern Wyoming in the late Oligocene and early Miocene, mantling the Precambrian cores of the Hartville Uplift and the Laramie Mountains (fig. 1). For over a century these deposits have yielded collections of fossil mammals defining an important biochronologic interval in the early Miocene of North America. Most skeletal remains represent isolated individuals, buried on ancient land surfaces by fine-grained, ash-rich eolian sediments. Ungulates (oreodonts, horses, camels, rhinoceroses) are most common as fossils, whereas predatory carnivorans at the apex of the ecological pyramid are rare. The largest and most imposing carnivores were beardogs of the family Amphicyonidae. Here I describe three species of early Miocene amphicyonids from the Upper Harrison beds of southeastern Wyoming (fig. 2): *Adilophontes brachykolos*, n. gen., n. sp., and *Daphoenodon*

falkenbachi, n. sp., based on previously unreported specimens collected from 1932 to 1940 in Goshen and Platte Counties by field parties of the Frick Laboratory, American Museum of Natural History (New York); and *D. skinneri*, n. sp., a single individual from Niobrara County, Wyoming, collected in 1957.

The Upper Harrison beds are the terminal formation of the Arikaree Group in the central Great Plains, and contain a fauna of latest Arikareean age (~18.8–19.2 Ma) in southeastern Wyoming, western Nebraska, and southwestern South Dakota. This rock unit has produced the richest representation of latest Arikareean mammals in North America, including a remarkable diversity of large carnivores. The amphicyonids serve as reliable biochronologic indicators of the concluding interval of the Arikareean North American Land Mammal Age in the Great Plains but at present are unknown elsewhere in North America.



Fig. 1. Fine-grained tuffaceous sandstones of the upper Arikaree Group mantling the granites and Paleozoic limestones of the Hartville Uplift in southeastern Wyoming (view to the southwest with Rawhide Butte at upper left and the Paleozoic carbonates of the Hartville Uplift on the far horizon). Arikaree outcrops east and north of Rawhide Butte include the Royal Valley district of C.H. Falkenbach.

ABBREVIATIONS

Anatomical

A	alisphenoid
BO	basioccipital
BS	basisphenoid
ex	exoccipital
gf	glenoid fossa
h	hypoglossal (condyloid) foramen
ina	bony tube for internal carotid artery
m	mastoid process
me	mastoid-exoccipital suture
p	petrosal promontorium
pc	posterior carotid foramen
pg	postglenoid foramen
pl	posterior lacerate foramen
pp	paroccipital process
R	?rostral entotympanic
s	basioccipital embayment for inferior petrosal venous sinus
SQ	squamosal
st	styliform process of the auditory bulla
T	ectotympanic
tt	tensor tympani fossa
w	posterior wall of the auditory bulla

Institutional

AMNH	American Museum of Natural History, New York
CM	Carnegie Museum of Natural History, Pittsburgh
FMNH	Field Museum of Natural History, Chicago
F:AM	Frick Laboratory, American Museum of Natural History, New York
LSUMG	Louisiana State University Museum of Geoscience, Baton Rouge, LA
UF	Florida Museum of Natural History, Gainesville, FL
UNSM	University of Nebraska State Museum, Lincoln, NE

GEOLOGIC AND GEOGRAPHIC DISTRIBUTION

The Upper Harrison beds were first named and described by O.A. Peterson (1907, 1909a) from prominent exposures in the Niobrara Canyon, Sioux County, northwest Nebraska (fig. 3). Hunt (1978, 1990) defined the northern and southern limits of the Upper

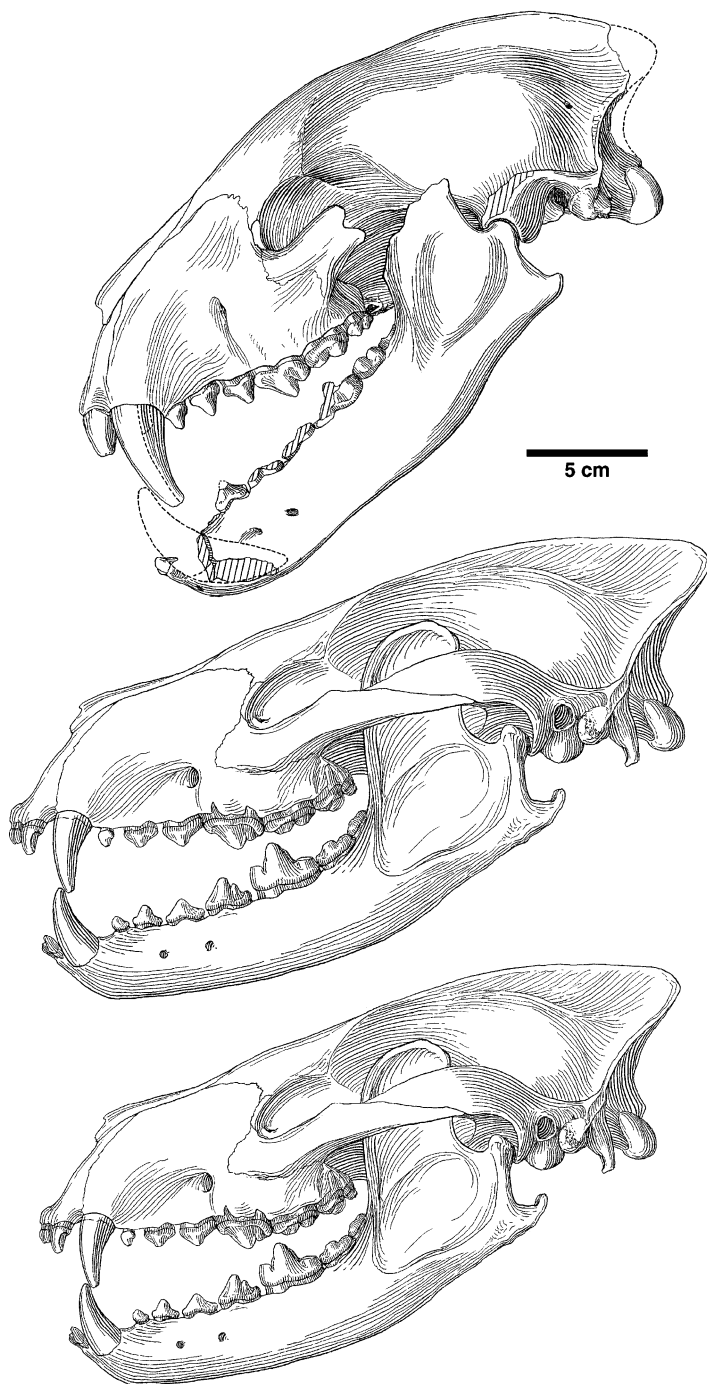


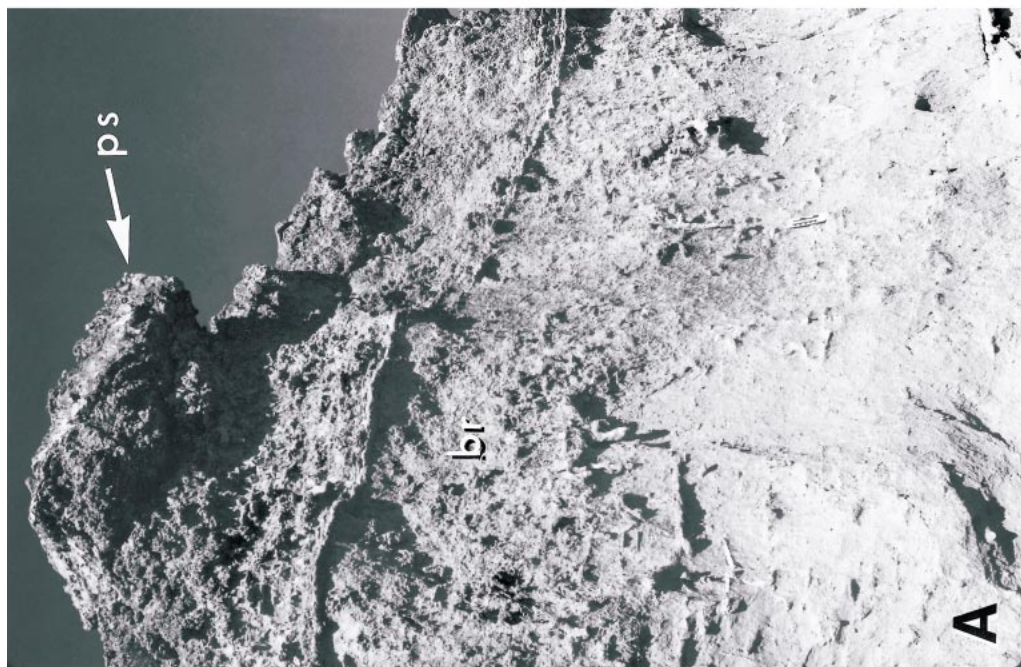
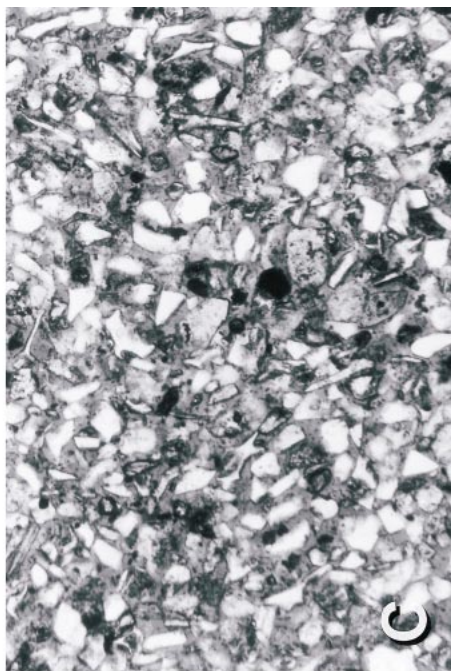
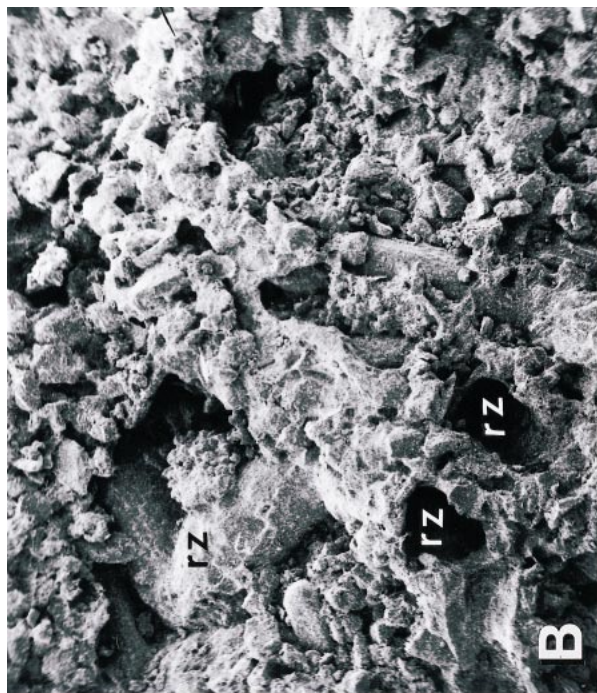
Fig. 2. Restorations of the skulls of amphi-cyonids from the Upper Harrison beds of southeastern Wyoming: **top**, *Adilophontes brachykolos*, n. gen., n. sp.; **middle**, *Daphoenodon falkenbachi*, n. sp.; **bottom**, *Daphoenodon skinneri*, n. sp. Scale bar, 5 cm.



Fig. 3. The Niobrara Canyon in northwest Nebraska was designated the stratotype area of the Upper Harrison beds by O.A. Peterson (1909a: 75); the canyon includes the thickest known exposures of the formation in Sioux County where siliceous paleosols form flat geomorphic surfaces (arrows) interpreted from their contained rhizoliths as regionally extensive grassland plains that extended westward to the Precambrian granite-cored Hartville Uplift.

Harrison in Sioux County, tracing the formation from Peterson's type area in the canyon north to the Pine Ridge and south to the Niobrara River valley at Agate Fossil Beds National Monument. Hunt's stratigraphic profile from the Pine Ridge escarpment to Agate in Sioux County indicated that the formation is thickest (~50 m) in the vicinity of the Niobrara Canyon and thins both to the north and south (Hunt, 1990: fig. 4). Upper Harrison beds extend eastward into Dawes and northern Sheridan Counties in Nebraska, where the sediments become noticeably finer grained. The beds continue to the northeast along the Pine Ridge of southwestern South Dakota where they had been identified as the Rosebud Formation by Macdonald (1963, 1970) and "Upper Rosebud" beds by Matthew (1907). The formation can be traced in outcrop from its type area in the Niobrara Canyon nearly continuously westward to the Hartville Uplift, and southward along the eastern margin of the uplift to the valley of the North Platte River. Outcrops of the Upper

Harrison continue south of the river and east of the Laramie Mountains to the vicinity of Chugwater, Platte County, Wyoming. Although the formation contains a variety of eolian, fluvial, and lacustrine lithofacies (Hunt, 1990), the fine-grained tuffaceous pale gray-brown to orange-brown eolian sandstones and siltstones predominate in the region, usually making up over 80% of outcrop. These eolian strata are punctuated at intervals by grassland paleosols, characterized by dense networks of fine (average diameter, 0.5 mm) anastomosed white silica rootlets that weather to siliceous duricrusts (fig. 4). The duricrusts form flat geomorphic surfaces that are particularly prominent east of the Hartville Uplift in southeastern Wyoming and northwestern Nebraska (fig. 3). The regional extent of these duricrusts and uniform expression of this lithofacies over several 1000 km² indicate the prevalence of open grassland or savanna east of the principal Precambrian-cored ranges in the early Miocene.



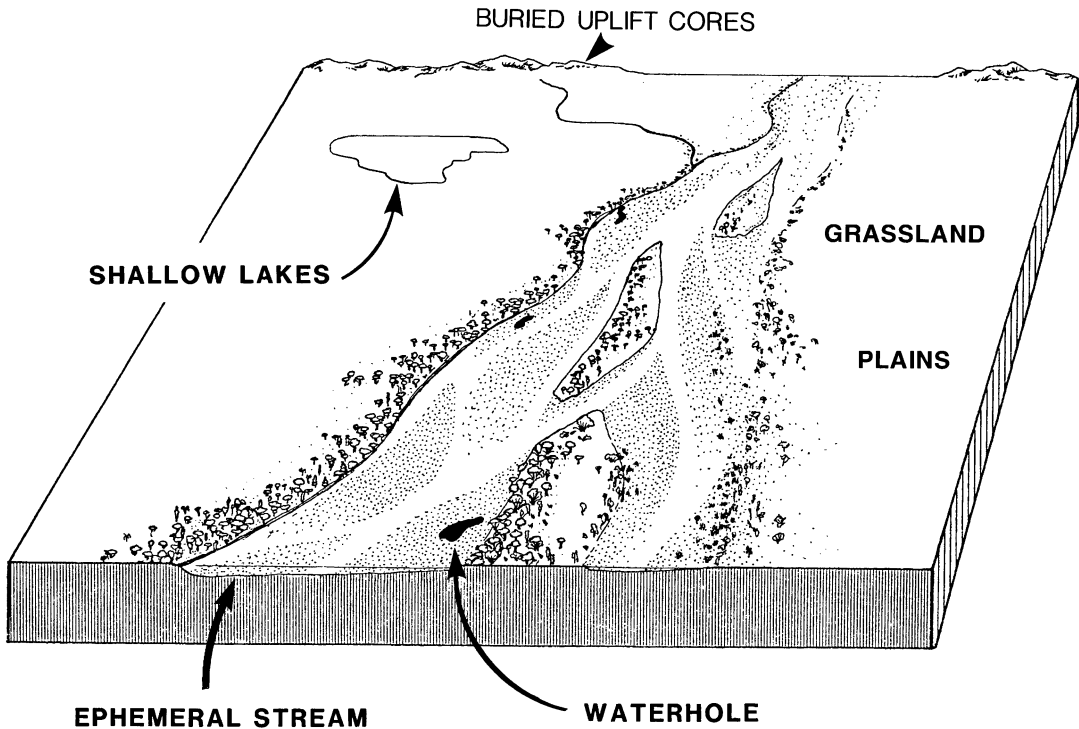


Fig. 5. Depositional environments of the early Miocene Upper Harrison beds in southeastern Wyoming and northwest Nebraska (from Hunt, 1990). Amphicyonid carnivores occur in stream, waterhole, and grassland plains but have not been found in ephemeral lakes.

Amphicyonids have been found not only in the grasslands but in all depositional environments of the Upper Harrison beds with the exception of a few shallow ephemeral lakes isolated on the open plains (fig. 5). No mammals have been found in these lacustrine limestones, which are sparsely populated by fossils of pulmonate gastropods, ostracods, aquatic plants, but are without fish or other aquatic vertebrates. Presumably the distribution of the amphicyonids in a variety of lith-

ofacies reflects their ability to range widely, occupying whatever settings offered suitable prey.

Two species of amphicyonids discussed here are among the largest predators of their time, approached in size by a carnivorous Upper Harrison mustelid *Megalictis ferox* (Hunt and Skolnick, 1996) and surpassed only by the large immigrant amphicyonine *Ysengrinia americana* (Hunt, in press a).

The geographic distribution of these am-

←

Fig. 4. A well-developed siliceous paleosol of the Upper Harrison beds, Agate Fossil Beds National Monument, Sioux County, Nebraska: **A**, tuffaceous fine-grained silty sandstone with siliceous paleosol (ps) at top of section forming duricrust; zone (br) of rhizoliths and invertebrate burrows gradually diminishes downward below duricrust (cliff height ~4.5 m). **B**, SEM photomicrograph showing sediment fabric of very fine sand and silt grains cemented by authigenic silica derived from pedogenic dissolution of volcanic glass shards and unstable mineral grains. Dense anastomosing networks of fine-diameter siliceous rhizoliths (rz, 0.5 mm) in these paleosols are interpreted as evidence of extensive grassland plains. **C**, Photomicrograph showing very fine tuffaceous sand and silt of Upper Harrison eolian lithofacies with abundant angular grains and volcanic glass shards. This lithofacies has produced large numbers of fossil mammals.

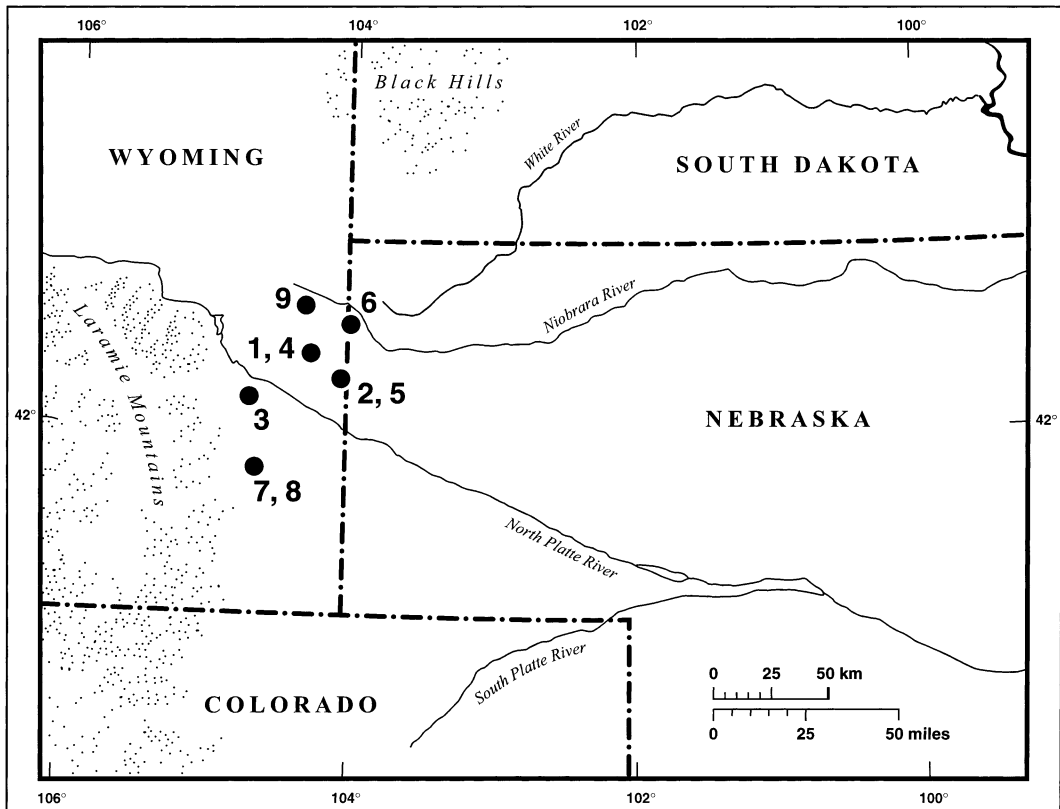


Fig. 6. Geographic distribution of *Adilophontes brachykolos*, *Daphoenodon falkenbachii*, and *D. skinneri* in the early Miocene Upper Harrison beds of southeastern Wyoming and western Nebraska. *A. brachykolos*: 1, F:AM 27568, 18 Mile District, Goshen Co., Wyoming; 2, F:AM 54140–54141, southwest of Spoon Butte, Goshen Co., Wyoming; 3, F:AM 54148, Roll Quarry, Platte Co., Wyoming. *D. falkenbachii*: 4, F:AM 54144, 18 Mile District, Goshen Co., Wyoming; 5, UNSM 99420, Lay Ranch beds west of Spoon Butte, Goshen Co., Wyoming; 6, CM 3719, Niobrara Canyon, Sioux Co., Nebraska; 7, 8, F:AM 54145–54150, 54146, 5–7 (~8–11.3 km) miles southeast of Chugwater, Platte Co., Wyoming. *D. skinneri*: 9, F:AM 70801, ~9 miles (14.5 km) southeast of Lusk, Niobrara Co., Wyoming. These amphicyonids are not known from Arikaree rocks in Colorado or South Dakota.

phicyonids in southeastern Wyoming and western Nebraska (fig. 6) is limited to the geographic extent of outcrops of the Upper Harrison and is essentially random within the outcrop area of the formation. The northernmost occurrences are in the Niobrara Canyon, Sioux County, Nebraska, and ~9 miles (14.5 km) southeast of Lusk, Niobrara County, Wyoming, and the southernmost ~5 miles (8 km) southeast of Chugwater, Platte County, Wyoming; they have not been found in younger rock units in the immediate area or elsewhere in North America.

Adilophontes brachykolos is represented

by three individuals; *D. falkenbachii* by remains of five individuals; and *D. skinneri* by one individual, reflecting how rarely these animals are discovered relative to the more commonly encountered fossil ungulates.

MAMMALS OF THE UPPER HARRISON BEDS

All but one specimen of the three species of amphicyonids described in this report come from Goshen, Platte, and Niobrara Counties, Wyoming. Unfortunately, the exact location where each was found remains un-

certain. Most were collected from 1932 to 1940 by personnel of the Frick Laboratory, American Museum of Natural History, New York, under the direction of Charles H. Falkenbach. Falkenbach's field parties were responsible for extensive collections of late Oligocene and early Miocene mammals from Arikaree strata in the vicinity of the Hartville Uplift in southeastern Wyoming during the decade prior to World War II (Galusha, 1975: 10f.).

Frick's collectors brought together a rich mammalian fauna from the Upper Harrison beds east of the Hartville Uplift in northern Goshen County, extending south and west into eastern Platte County. This fauna includes a homogeneous assemblage of early Miocene taxa: the oreodonts *Merychys* and *Merycochoerus matthewi*; equids *Parahippus nebrascensis*, *P. wyomingensis*, and an anchitherid; camels *Tanymycter*, *Oxydactylus*, and *Stenomylus*; rhinoceroses *Menoceras* and *Diceratherium*; the large entelodont *Dinohyus*; and the chalicotherid *Moropus*. Among the small and mid-sized carnivorans were canids (*Desmocyon thomsoni*, *Osbornodon brachypus*, *Cynarctoides luskensis*), the mustelid *Promartes*, and the hemicyonine ursid *Cephalogale*. The large carnivorans were primarily amphicyonids: the immigrant amphicyonine *Ysengrinia*; several species of the endemic daphoenines *Daphoenodon* and *Adilophontes*, described here; at least two species of temnocyonines; and the predatory palearctid *Megalictis*. *Adilophontes*, *Ysengrinia*, and one of the temnocyonines were the largest of these carnivores, the males probably attaining a body mass of ~60–>100 kg.

The notable absence of highly cursorial ungulates of large size in the Upper Harrison fauna finds a parallel in the lack of large digitigrade carnivores. Ruminant artiodactyls and oreodonts were mostly small, and were probably frequent prey of the beardogs. Horses and camels were larger on average and would have presented a greater challenge to these carnivores. Adult entelodonts, chalicotheres, and diceratherid rhinoceros should have been to some degree immune to predation by amphicyonids because of their size, with the exception of their vulnerable young. Bones of calves of the small rhinoceros *Men-*

oceras and the small oreodont *Merychys* have been found in beardog dens in the region (Hunt et al., 1983).

SYSTEMATIC PALEONTOLOGY

ORDER CARNIVORA BOWDICH, 1821

DIVISION ARCTOIDEA FLOWER, 1869

FAMILY AMPHICYONIDAE TROUESSART, 1885

SUBFAMILY DAPHOENINAE HOUGH, 1948a

Adilophontes, new genus

TYPE SPECIES: *Adilophontes brachykolos*, new genus and species.

ETYMOLOGY: *adeilos*, fearless; *phontes*, slayer, Greek; in reference to its carnivorous habit.

INCLUDED SPECIES: Only the type species.

KNOWN DISTRIBUTION: Latest Arikareean, Goshen County and Platte County, Wyoming.

DIAGNOSIS: As for the monotypic species.

DISCUSSION: The genus is based upon rare occurrences of a large carnivorous amphicyonid from the Upper Harrison beds of southeastern Wyoming, at present recognized nowhere else in North America. Each of the three known individuals includes a well-preserved skull with mandible, and some associated postcranial elements. Limb bones and metapodials demonstrate lower forelimbs and feet that were short relative to the size of the skull. Males have large skulls accompanied by a radius with a distal exostosis; a small skull associated with a radius without an exostosis is considered female. The radial exostosis is not a pathologic feature but is a normal osteological characteristic of several daphoenine species (e.g., *Daphoenus vetus*, *Daphoenodon superbus*, *Daphoenodon notionastes*).

Adilophontes brachykolos, new species

Figures 2A, 7–17, 25B

HOLOTYPE: F:AM 27568, complete uncru-
shed skull and mandibles, left humerus, ulna
and radius (without exostosis), proximal left
femur, distal right tibia, both astragali, left
navicular and ectocuneiform, four lumbar
vertebrae and numerous fragments (figs. 7,
8B, 10A, C).

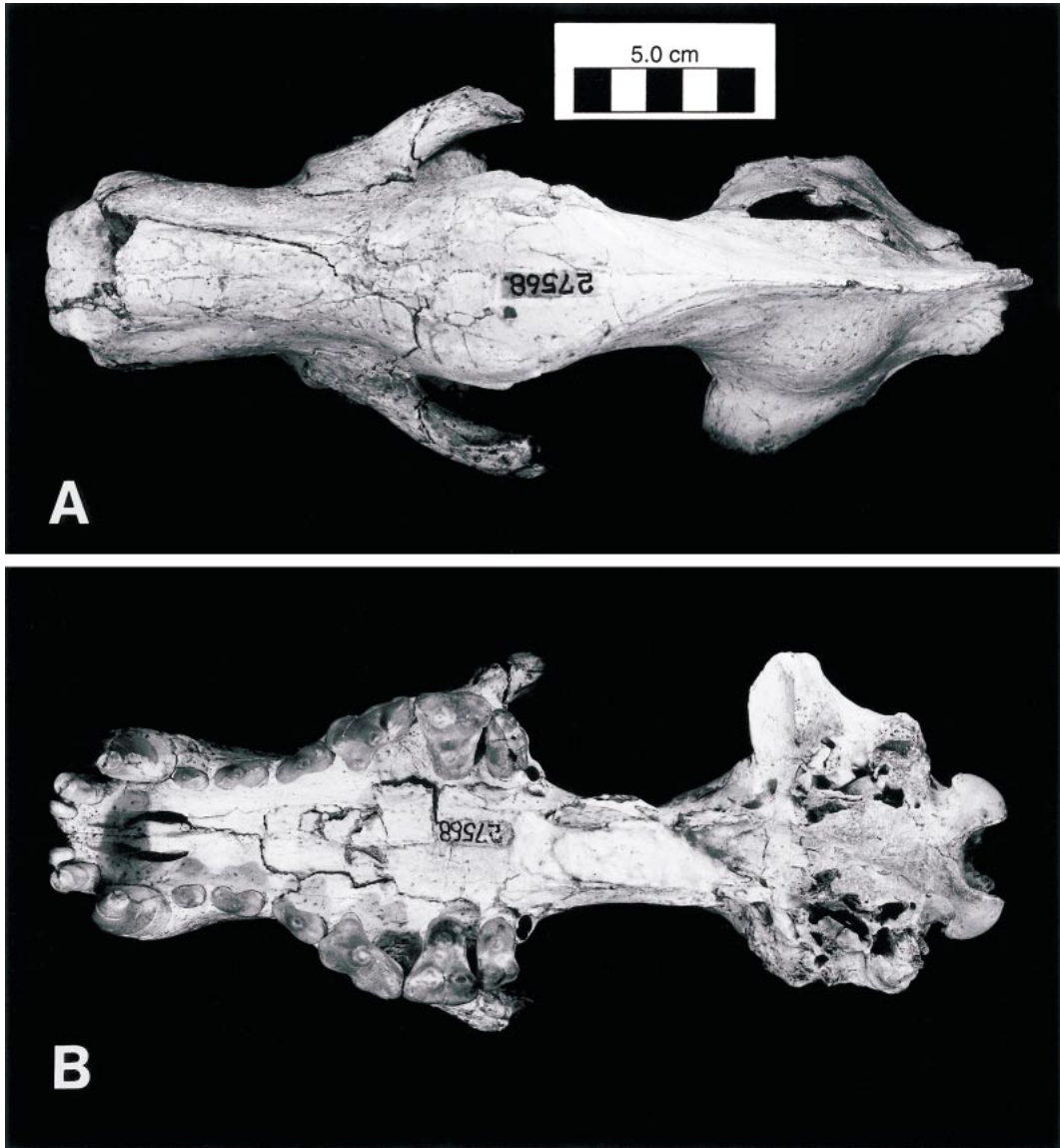


Fig. 7. Holotype skull of *Adilophontes brachykolos*, F:AM 27568, Upper Harrison beds, 18 Mile District, Goshen Co., Wyoming: **A**, dorsal view; **B**, palatal view. Scale bar, 5 cm.

ETYMOLOGY: *brachykolos*, Greek, short-legged, in reference to the short forelimb of the species, based on the radii associated with two of the skulls (F:AM 27568, F:AM 54140).

TYPE LOCALITY: Approximately 18 miles (29 km) southeast of Lusk, Goshen County, Wyoming (18 Mile District of C.H. Falkenbach).

TYPE HORIZON: Upper Harrison beds, upper Arikaree Group (early Miocene).

REFERRED SPECIMENS: (1) F:AM 54140, complete skull, slightly crushed, associated with distal femur, left radius (with distal exostosis), left calcaneum, three articulated cervical vertebrae, vertebral fragments, left metatarsal 3, left metatarsal 4, proximal metatarsal 5, from southwest of Spoon Butte,

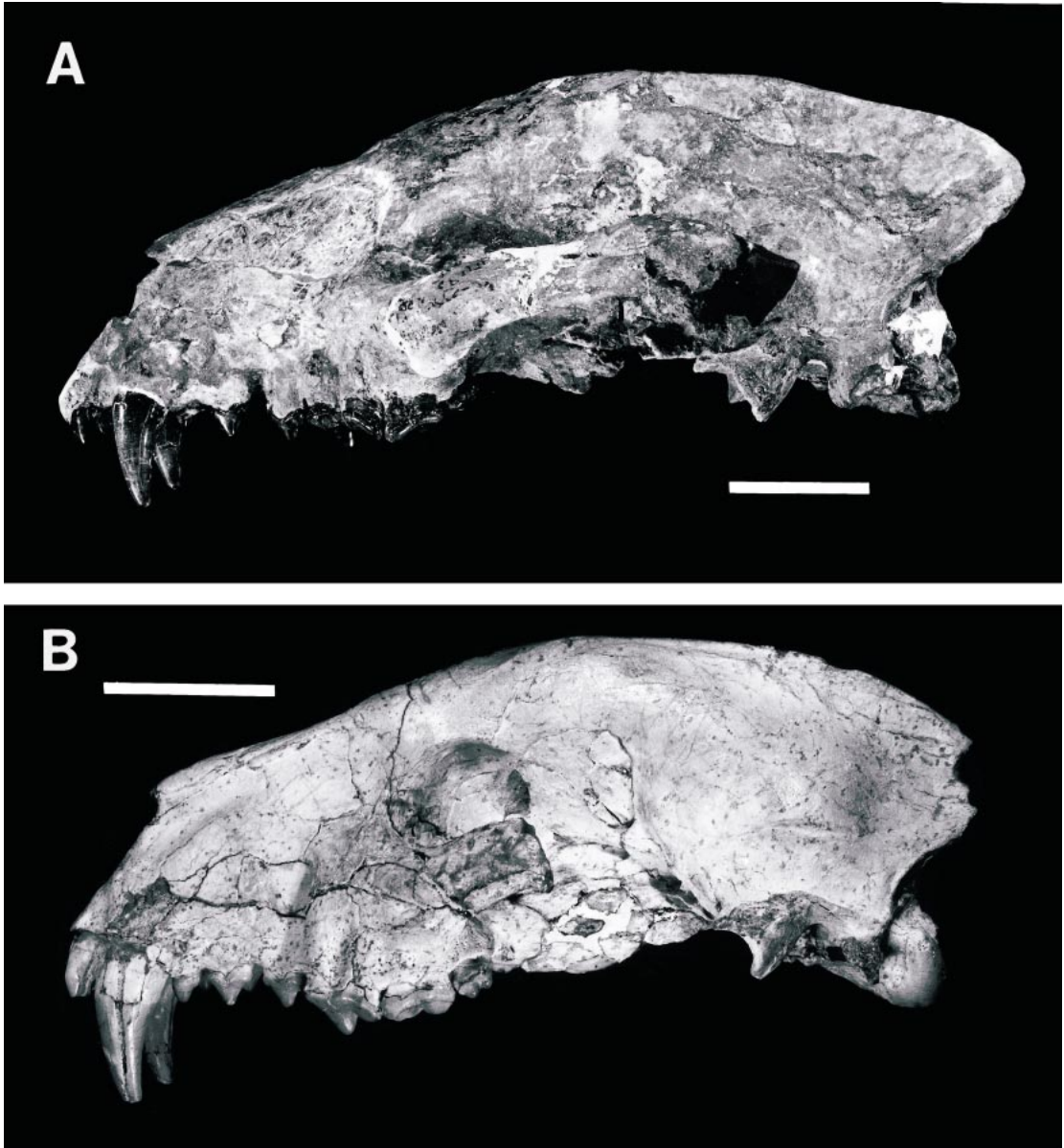


Fig. 8. *Adilophontes brachykolos*: **A**, male cranium, F:AM 54140, Upper Harrison beds, southwest of Spoon Butte, Goshen Co., Wyoming; **B**, female cranium, F:AM 27568, holotype, Upper Harrison beds, 18 Mile District, Goshen Co., Wyoming. Scale bars, 5 cm.

Goshen Co., Wyoming (figs. 8A, 9, 10B, 11); F:AM 54141, a damaged right mandible with m1–3 and p4 fragment, from the same locality as F:AM 54140 and probably the same individual; (2) F:AM 54148, complete skull and associated mandibles, atlas vertebra, left femur, and a distal metapodial (?left metatar-

sal 4), from Roll Quarry, about 3 miles (4.8 km) south of Guernsey, Platte County, Wyoming (figs. 12, 13).

KNOWN DISTRIBUTION: Latest Arikareean, Goshen County and Platte County, Wyoming.

DIAGNOSIS: Mid-sized to large amphicyon-

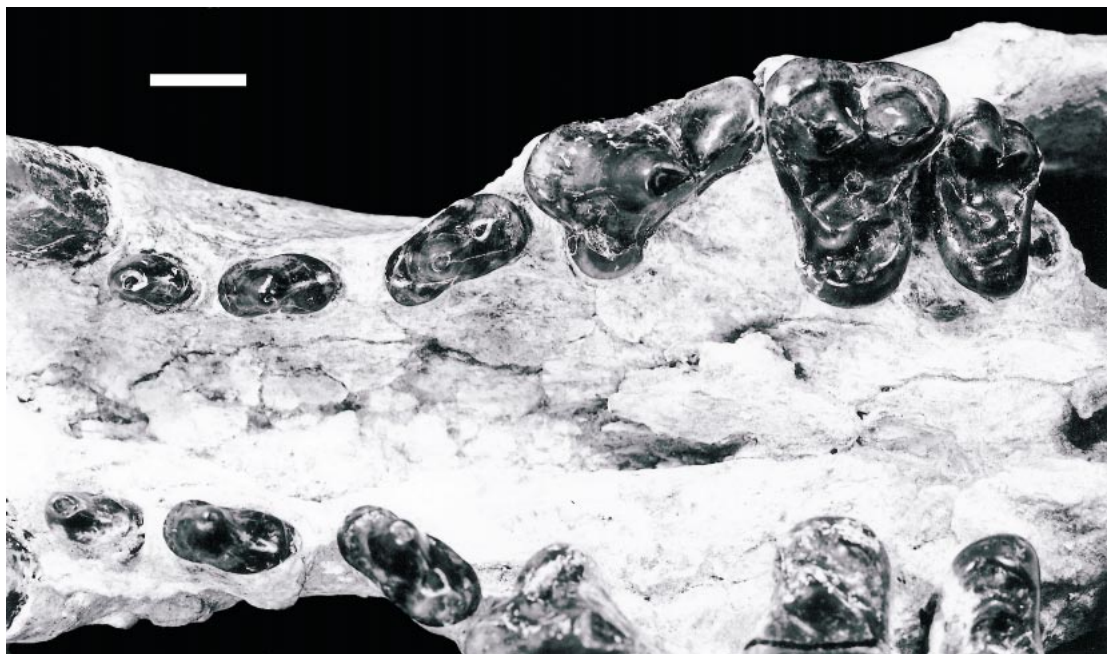


Fig. 9. *Adilophontes brachykolos*, F:AM 54140, upper dentition and palate of adult male, Upper Harrison beds, southwest of Spoon Butte, Goshen Co., Wyoming. *Adilophontes* retains fully developed premolars in contrast to the reduced premolars of the amphicyonine *Ysengrinia*, which also occurs in Upper Harrison beds at Spoon Butte. Scale bar, 1 cm.

ids with long, narrow dolichocephalic skulls, dorsoventrally deep (in contrast to *Daphoenodon superbus*, in which the skull is low and broad); rostrum deep; epipodial limb segments short, not elongated as in some amphicyonid species; distal radius with prominent exostosis in males (the exostosis does not occur in *Ysengrinia* and *Amphicyon*); metapodials short, not elongated as they are in temnocyonines; premolars well-developed, not reduced as in *Ysengrinia*; dental formula 3-1-4-3/3-1-4-3; M2 not enlarged relative to M1; p2 and p3 longer (also p1-4 length) than the corresponding premolars of *Daphoenodon superbus* and *Ysengrinia*.

DISCUSSION: The three individuals assigned to this species are interpreted as two large males and a smaller female: (1) F:AM 54140, a mature male, represented by a skull (basilar length, ~30 cm), radius, distal femur, partial hindfoot, and several vertebrae, from west of Spoon Butte, Goshen County, Wyoming (F:AM 54141, a partial mandible which shows the same preservation as the skull and corresponds in size also comes

from west of Spoon Butte, and probably belongs to the same individual as F:AM 54140); (2) F:AM 54148, an aged male skull (basilar length, 30.5 cm), both mandibles, and femur, from Roll Quarry, Platte County, Wyoming, associated with a number of other mammals (rhinoceros *Menoceras*, equid *Parahippus*), apparently in a local bonebed; (3) F:AM 27568, the holotype, a mature female skull (basilar length, 24.3 cm), two heavily damaged mandibles, associated with a partial forelimb including the radius, and a partial hindfoot (astragalus, navicular, ectocuneiform) from the 18 Mile District of Falkenbach, Goshen County, Wyoming. The skull of F:AM 54140 is associated with a radius that has a prominent bony distal exostosis (fig. 10B). The smaller skull of F:AM 27568 is accompanied by a radius without an exostosis (fig. 10A). F:AM 27568 and 54148 both retain the basicranium and remnants of the auditory bulla, which are useful in determining phylogenetic relationships of carnivorans.

Although the precise localities at which

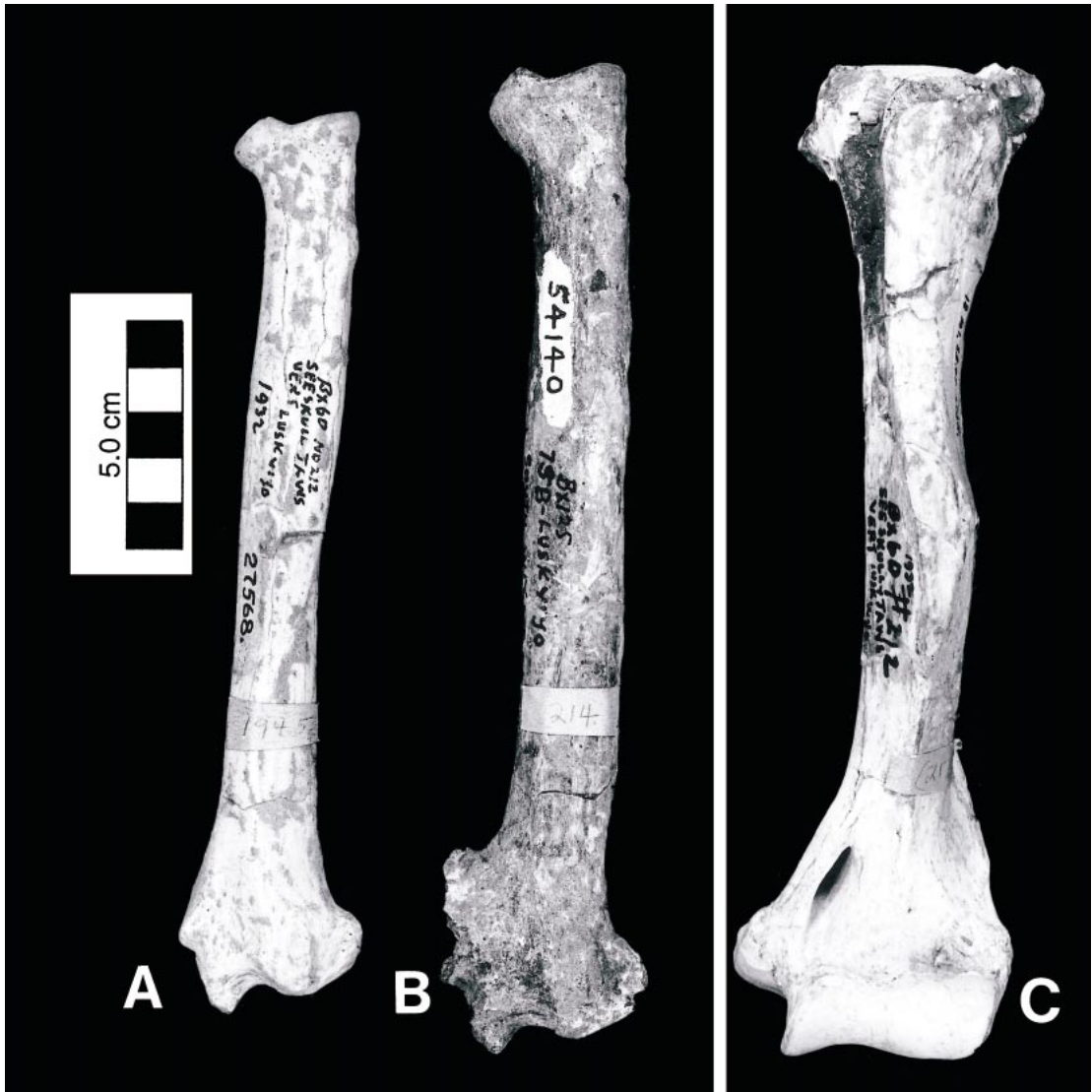


Fig. 10. Forelimb bones of *Adilophontes brachykolos* associated with female and male skulls of figure 8: **A**, female radius lacking distal exostosis, F:AM 27568, holotype; **B**, male radius with distal exostosis, F:AM 54140; **C**, female humerus, F:AM 27568, associated with holotype radius. Scale bar, 5 cm.

the three individuals of *Adilophontes* were found were not recorded by the Frick Laboratory field collectors, identification of the approximate locations can be based on recent field studies of the same geographic areas. Two of the three individuals (F:AM 27568, F:AM 54140–54141) from the Upper Harrison beds in northern Goshen County can be placed fairly accurately in a modern stratigraphic context.

F:AM 54140 was collected from an area “southwest of Spoon Butte” in Goshen County. Spoon Butte is a commanding north–south-oriented topographic feature in northeastern Goshen County, 3.4 miles (5.7 km) in length and 0.6 miles (1 km) in width at several points; it is intersected by the Wyoming–Nebraska state boundary. Rising 400 ft above the surrounding terrain, the flat-topped butte is held up by a thick (~20 ft)

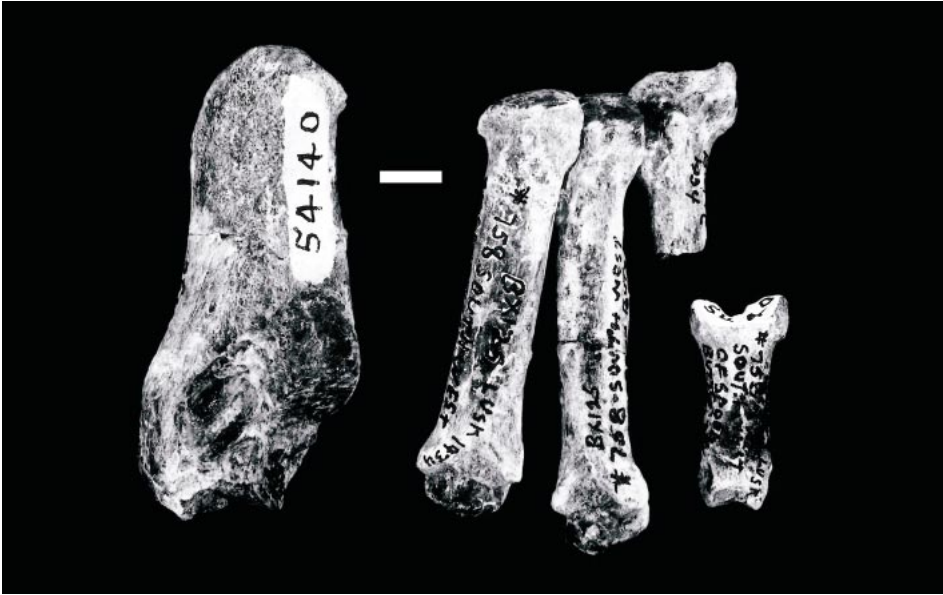


Fig. 11. Partial hindfoot of *Adilophontes brachykolos* associated with the male cranium, F:AM 54140, from left to right: calcaneum, metatarsals 3, 4, and proximal part of 5, all of the left side, and a proximal phalanx. Scale bar, 1 cm.

caprock of mid-Miocene fluvial sandstone representing a linear remnant of a major fluvial system in reversed topographic mode. Our geologic mapping of the butte and the surrounding region (R.M. Hunt, Jr., Open-File Map, Spoon Butte 7.5-minute quadrangle, University of Nebraska Conservation

and Survey Division, Lincoln, NE) discovered an early Miocene paleovalley fill, 2 miles (3.2 km) in width, passing through the butte from west to east, and extending for a considerable distance beyond the butte itself. These early Miocene strata yielded a latest Arikareean mammal fauna to UNSM field



Fig. 12. Cranium of an aged adult male *Adilophontes brachykolos* with heavily worn teeth, F:AM 54148, Upper Harrison beds, Roll Quarry, Platte Co., Wyoming. Scale bar, 5 cm.

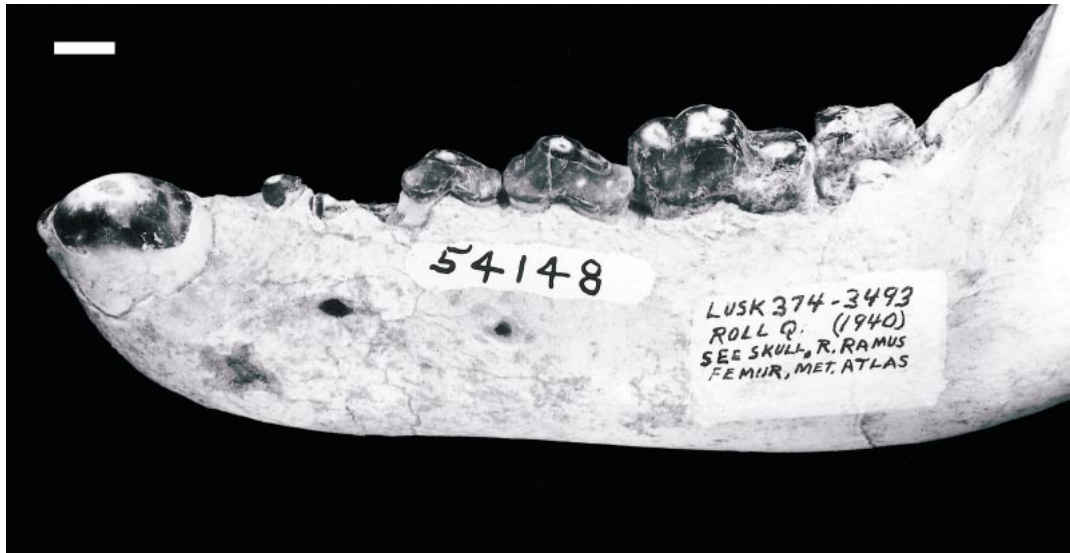


Fig. 13. Left mandible of *Adilophontes brachykolos* associated with cranium in figure 12, F:AM 54148; note worn premolars, molars, and blunted canine. Similar toothwear has been observed in aged North American wolves (*Canis lupus*). Scale bar, 1 cm.

workers and comprise fluvial channel and floodplain units of fine-grained tuffaceous sandstones, siltstones, and lithic pebble gravel, age-equivalent to the Upper Harrison beds. Because this paleovalley fill is geographically isolated from the main body of the Upper Harrison beds to the north in northern Goshen County (Lone Sand Hill 7.5-minute quadrangle), the strata have been informally named the Lay Ranch beds (Hunt, 1985a; Skolnick, 1985). The Lay Ranch beds are the only fossiliferous formation likely to have produced this amphicyonid carnivore (F:AM 54140–54141). A sediment sample removed from the skull, a fine-grained brownish-gray tuffaceous sand with abundant dark minerals scattered through the matrix, is comparable to similar samples taken from Lay Ranch outcrops west and southwest of Spoon Butte.

F:AM 27568 came from Upper Harrison outcrops approximately 18 miles (29 km) southeast of Lusk, Wyoming, that Falkenbach designated the “18-Mile District”. This district lies east of Route 85 in northern Goshen County. Most of the exposures are fine-grained eolian tuffaceous sandstones overprinted at various levels by siliceous paleosols, referable to a volcanoclastic loess lith-

ofacies (Hunt, 1990: 75f.). Sediment samples taken from this lithofacies and from F:AM 27568 are comparable: a fine brownish-gray tuffaceous sand with dark minerals scattered through the rock matrix.

Mammalian fossils found in the 18 Mile District and in the Lay Ranch paleovalley commonly occur as partial skeletons of single individuals, with some bones still articulated. The skeletons accumulated on land surfaces of semiarid grassland plains (18 Mile District) and in shallow channels and the floodplain of a broad ephemeral stream (Lay Ranch paleovalley), where they were scavenged and scattered prior to burial by gradually accumulating fine-grained tuffaceous sediments. The partial skeletons of F:AM 27568 and F:AM 54140–54141 conform to this taphonomic mode.

The burial environment of the Roll Quarry individual (F:AM 54148) from Platte County south of Guernsey, Wyoming, is more difficult to interpret because the exact quarry location is lost. American Museum field records do not establish its geographic location, only that the quarry was sited “3 miles south of Guernsey, Wyoming”. Fortunately, a plaster-jacketed block of fossils in the original sediment matrix from the quarry sur-

vives at the American Museum. It includes the mixed skeletal remains of horse and rhinoceros, evidently part of a mass accumulation buried either in a waterhole or local fluvial channel. A stratigraphic section made by C.H. Falkenbach in the AMNH archives, as well as the associated fauna from Roll Quarry, suggests that the quarry was either in the Upper Harrison beds or an unidentified overlying stratigraphic unit. A personal reconnaissance in October 2001 of Arikaree rocks south of Guernsey demonstrated the presence of Upper Harrison lithologies that conform to Falkenbach's stratigraphic section and lithic descriptions but failed to locate the quarry. However, examination of sediment samples from the Roll Quarry skull, and sediment removed from the other skulls of *Adilophontes* (F:AM 27568, 54140), shows a uniform mineralogy: a fine, brownish-gray, silty tuffaceous sandstone of similar petrographic composition, typical of the Upper Harrison beds of southeastern Wyoming. All of these samples, including one removed from the Roll Quarry skull, contain unusual elongated angular laths of glassy black obsidian that have not been observed in overlying rock units, and therefore suggest that Roll Quarry does occur in the Upper Harrison beds.

When these three individuals were collected in the period 1932–1940, they were informally referred to *Daphoenodon* by the Frick Laboratory. However, the laterally compressed skulls of *Adilophontes*, with their deep rostra and more rounded dorsal profile, differ markedly from the low, broad skulls of *Daphoenodon* (fig. 2). These differences in skull form, together with the short forelimb and a dentition with well-developed premolars, distinguish *A. brachykolos* from other Arikareean amphicyonids: all temnocyonine amphicyonids have elongated lower limbs and feet; the daphoenines *D. superbis* and *D. falkenbachii* differ in their low, broad skulls; and the amphicyonines *Ysenegrinia* and *Amphicyon* have much reduced anterior premolars.

Postcranial bones associated with two of the skulls of *Adilophontes* demonstrate that, despite their large size, these carnivores were short-legged, evidenced by the proportions of radius and metapodials relative to the humerus. The lengths of humerus (222 mm)

and associated radius (199 mm) of the holotype of *A. brachykolos* indicate a humero-radial index of 89.6 (fig. 10A, C), similar to that of the amphicyonines *Ysenegrinia americana* (~89.3) and *Cynelos lemanensis* (~89.5). This ratio in *D. superbis* is 86.7. In living lions (*Panthera leo*, 90–94, N = 11) and digitigrade canids (*Canis lupus*, *C. latrans*, 97–104, N = 7) this ratio consistently is >90, indicating a more elongate forelimb.

The degree of elongation of the manus relative to the radius is not known in *Adilophontes* because of the absence of metacarpals. However, in amphicyonids the forefoot is usually shorter than the hindfoot, and a short hindfoot is evident in *A. brachykolos* (F:AM 54140) based on the length of MT3–4 (73.2, 78.6 mm) relative to the length of its associated calcaneum (80.9 mm) and radius (218 mm). Associated hindfeet of the smaller *D. superbis* (CM 1589c: MT3–4, 73.1, 77.2 mm; calcaneum, 63.3 mm; CM 1589, holotype: MT3–4, 70, 73 mm; calcaneum, 59.1 mm) from the Agate Monument carnivore dens have metatarsals of almost the same lengths, but much less robust, and a much smaller calcaneum, indicating a relatively larger but quite short hindfoot in *A. brachykolos* (fig. 11).

Although the two large skulls of *Adilophontes* (F:AM 54148, 54140) differ conspicuously in size (basilar lengths, 30.5 cm, ~30 cm) from the smaller skull of the holotype (~24 cm, F:AM 27568), the upper toothrows of these three individuals are much more similar in size (C–M2 length: 13.2, 12.1, 11.4 cm, respectively). The marked size difference in the skulls is probably attributable to sexual dimorphism, an inference supported by the osteology of the radius. The smaller skull of the holotype (F:AM 27568) is accompanied by a short radius without an exostosis (fig. 10A); one of the larger skulls (F:AM 54140) is also associated with a short radius but with a prominent exostosis (fig. 10B). Males of daphoenine amphicyonids are known to have such exostoses on the distal radius that are lacking in females (Hatcher, 1902; Hunt, 1996: 483). Despite the ~6 cm difference in basilar length between F:AM 27568 and F:AM 54140, the lengths of their radii are similar (F:AM 27568, 19.9 cm; F:AM 54140, 21.8 cm). The

ratio of radius length/basilar length of skull in F:AM 27568 is 82.5, and in F:AM 54140 is 72, indicating the relatively larger size of the head in the male. Here these specimens are considered a single species, and *A. brachykolos* is identified as a short-legged carnivorous amphicyonid with large, robust males and smaller-skulled females (fig. 14).

The basicranium of the holotype (F:AM 27568) is well-preserved (fig. 15), and although crushed, a comparable basicranial anatomy occurs in one of the referred male skulls (F:AM 54148). The basioccipital is broad, 30.4 mm in the holotype; width across the mastoid processes is 78.3 mm. The proportions in F:AM 54148, the large male, are similar, but crushing precludes accurate measurements. The form of the basicranial bones surrounding the auditory region in both male and female is the same: the glenoid fossae lie on the same plane as the basicranial axis; and the basicranial axis forms an angle of $\sim 30^\circ$ with the palate, demonstrating that the face of this carnivore was somewhat depressed (fig. 2A), allowing the orbits to be more forwardly directed (this angle is $\sim 15^\circ$ in *D. superbus*). The roof of the external auditory meatus formed by the squamosal is 17.6 mm in width, and internal to this, the petrosal is deeply inset in the auditory area; the mastoid processes are well-developed but small relative to the size of the skull, and the paroccipital processes are very small. The lateral margin of the basioccipital is deeply embayed for an enlarged inferior petrosal venous sinus, presumably containing a loop of the internal carotid artery as in living ursids (Hunt, 1974). The postglenoid foramen is moderately developed for internal jugular drainage; the hypoglossal foramen lies relatively close to the posterior lacerate foramen.

Perhaps the most striking aspect of the basicranium in this species is that it is so small relative to the overall dimensions of the skull (fig. 7B). In the holotype female (F:AM 27568) the ratio of basicranial width (measured across the mastoid processes) to basilar length of skull is $78.3/243$ mm, or 0.32; for the large male of *A. brachykolos* this ratio is $\sim 92/305$ mm, or 0.30; in the female holotype of *D. superbus* this ratio is $80.4/215$ mm, or 0.37. In overall dimensions, the basicranium of *A. brachykolos* is short and rather narrow

relative to *D. superbus*, and a visual inspection of the skulls of *A. brachykolos* confirms this impression: the elongate, narrow skull (fig. 7) includes a small basicranium coupled to a large rostrum with a particularly robust dentition.

The auditory bulla is largely intact in the holotype except for the loss of the ventral floor (figs. 15, 16). As in other early Miocene amphicyonids, the bulla was a rudimentary flask-shaped bony capsule. Formed mostly or entirely by the ectotympanic bone, its walls are thin and very delicate. The bulla protruded below the level of the basicranial axis and so was susceptible to breakage. The large male (F:AM 54148, fig. 17) retains more of the ventral floor of the bulla than the holotype female; its shape and modest degree of inflation are similar to the bulla of the *D. superbus* holotype (fig. 18, CM 1589). The anterior part of the bulla is strongly extended into the anteromedial corner of the auditory region and includes a lathlike styliiform process. As in *D. superbus*, the anterior part of the bulla is prolonged ~ 2 to 8 mm in front of a transverse line drawn through the postglenoid processes. In contrast to the evident anterior extension of the bulla, the posterior wall is quite thin and uninflated; it does not extend behind the mastoid processes, an indication that the bulla remains in a rudimentary form typical of early arctoid carnivorans. This bulla form is closely approximated by living ursids which, however, have an even more strongly ossified posterior wall than seen in these beardedogs (Hunt, 1974: pl. 4).

The internal structure of the bulla can also be seen in the holotype female (fig. 16). The interior of the right auditory region is essentially intact. Here, and in F:AM 54148, a short bony external auditory meatus ~ 8 mm in length was probably continued laterad by cartilage in the living animal. The middle ear cavity is rather long and narrow, 5.5–7.5 mm in width in the holotype, and possibly as much as 1 cm in the large male. The length of the middle ear cavity in the holotype is ~ 20 mm and in F:AM 54148 is ~ 24 mm; the cavity is a single chamber. The crista tympanica is nearly vertical, with the plane of the tympanum tilted inward $\sim 15^\circ$ and rotated slightly mesad. Ventral to the crista the

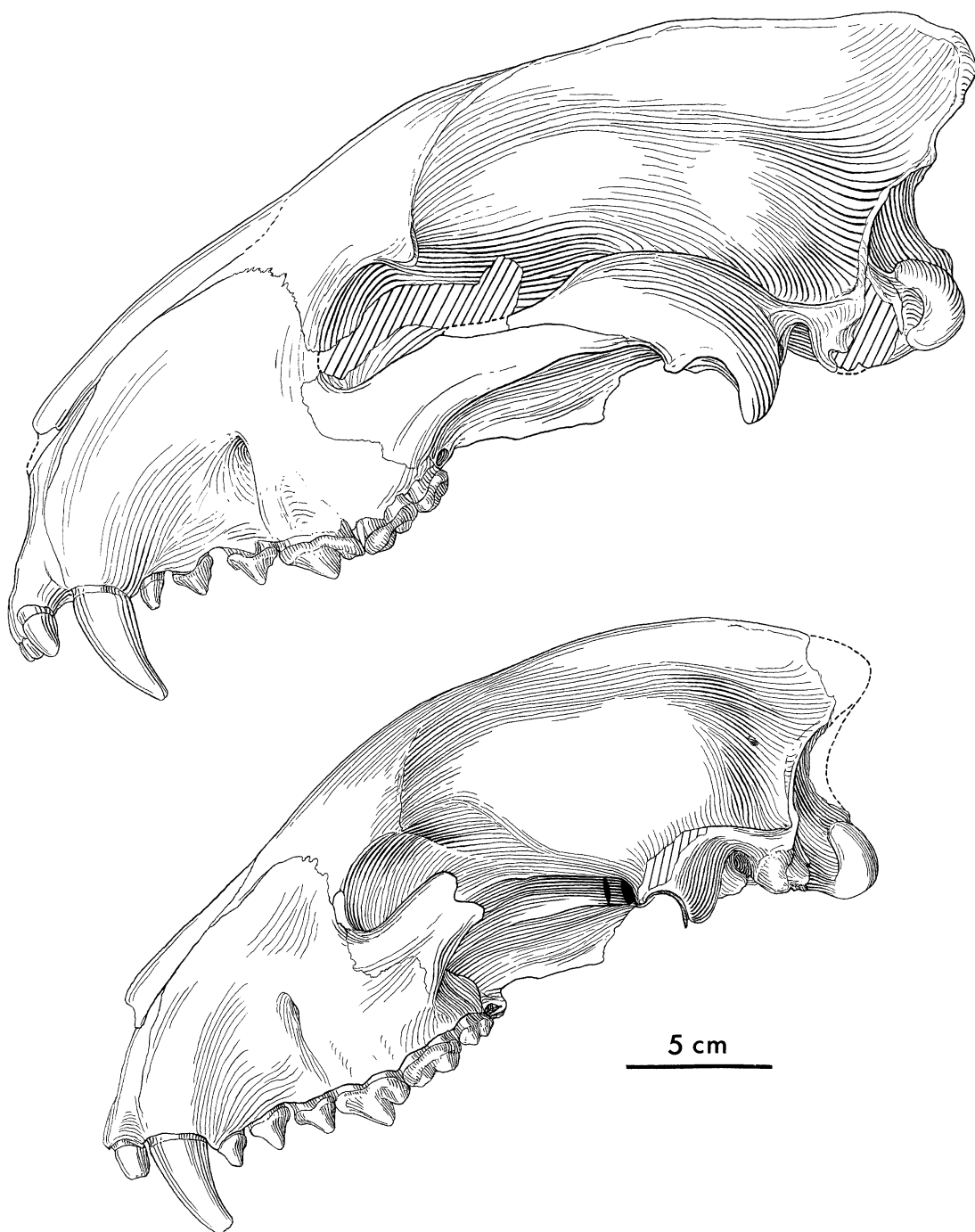


Fig. 14. Restoration of male and female crania of *Adilophontes brachykolos* from the Upper Harrison beds, Goshen Co., Wyoming: **top**, male, F:AM 54140; **bottom**, female, F:AM 27568. Scale bar, 5 cm.

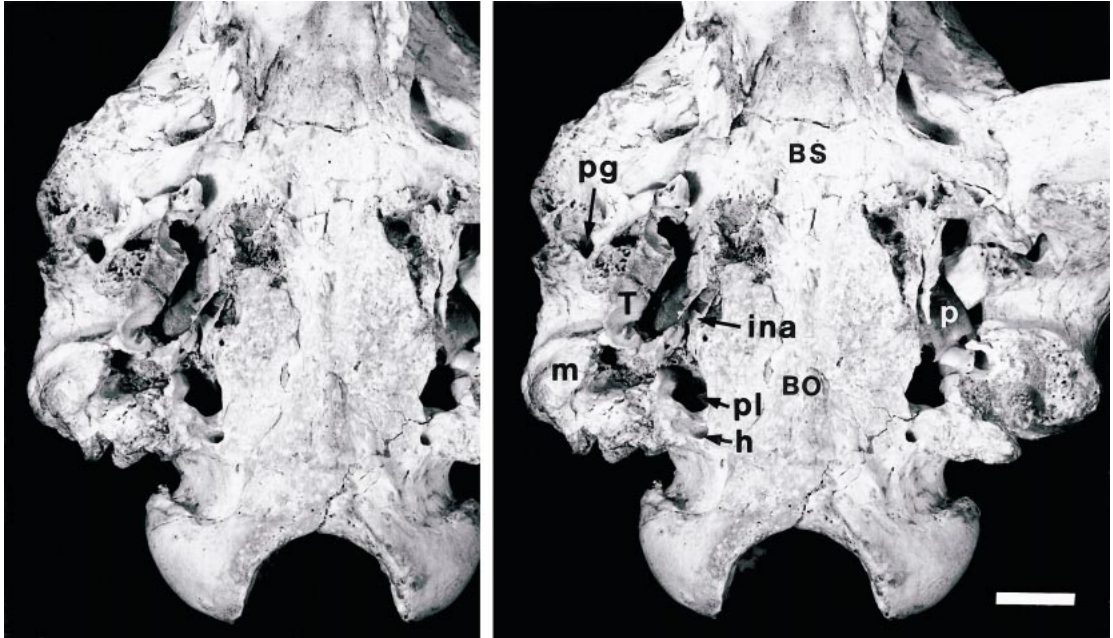


Fig. 15. Basicranium of *Adilophontes brachykolos*, holotype, F:AM 27568, Upper Harrison beds, Goshen Co., Wyoming. Stereophotographs. Scale bar, 1 cm. For abbreviations in this and all subsequent anatomical figures, see p. 3.

middle ear cavity has been extended laterad a short distance into the bony external auditory meatus; this space is confluent with an extension of the middle ear cavity into the anterolateral bulla wall that produces a small pocket (figs. 15, 16). This pocketing also occurs in *Daphoenodon falkenbachii* (fig. 23A) and is a shared derived trait characteristic of

both *Adilophontes* and *Daphoenodon*. The pocketing is also present in the earliest North American *Amphicyon*, in which it is much more extensively developed. We now know that this type of middle ear extension evolved in parallel in several lineages of early Miocene amphicyonids.

The internal carotid artery traveled the en-

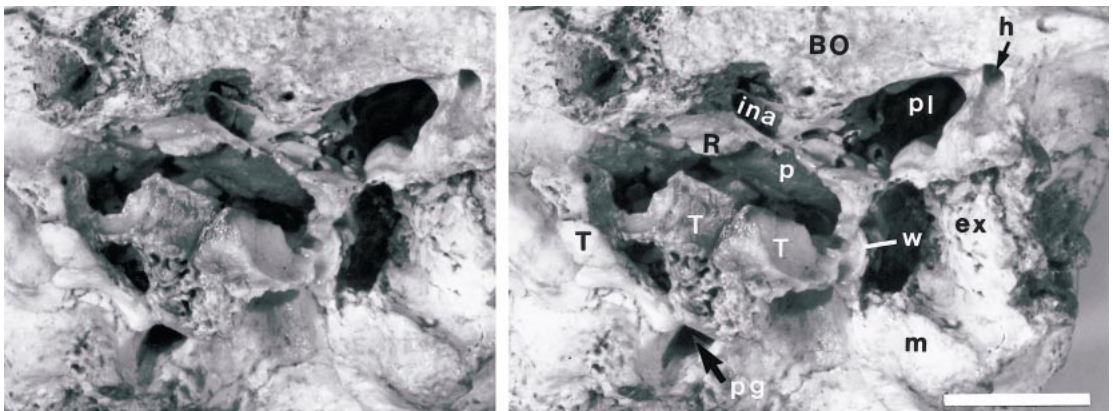


Fig. 16. Stereophotographs of the right auditory region of *Adilophontes brachykolos* (anterior to left), F:AM 27568, female holotype, Upper Harrison beds, Goshen Co., Wyoming. Scale bar, 1 cm.

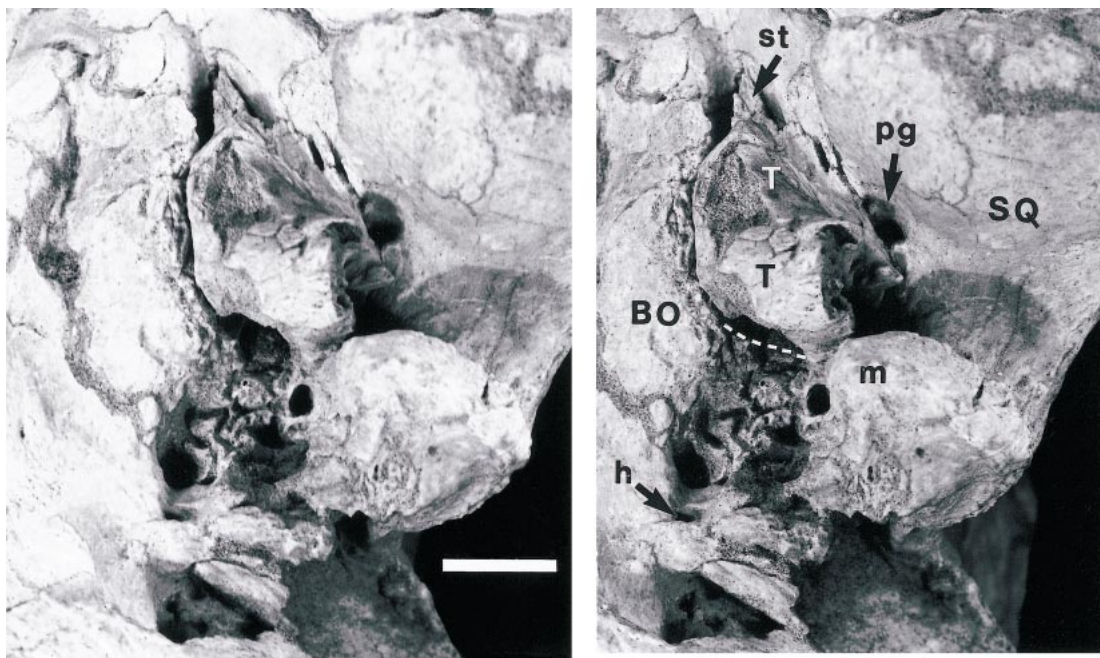


Fig. 17. Stereophotographs of left auditory region of aged male *Adilophontes brachykolos* (anterior at top), F:AM 54148, showing auditory bulla in place. White dashed line indicates the location of the posterior bulla wall which has been lost to breakage in this individual. Note that the bulla does not extend behind the mastoid process. Scale bar, 1 cm.

tire length of the medial wall of the bulla enclosed in a thin-walled bony tube. This bony tube rested directly on the medial margin of the petrosal promontorium (figs. 15, 16). The artery entered the tube at the posteromedial corner of the bulla, as in many living ursids (Hunt, 1974: pl. 4, fig. 16), and not farther forward along the medial wall, as in most living mustelids and procyonids. It continued within the tube to the anteromedial corner of the auditory region, where it traveled the ventral margin of a small triangular ossification situated on the anterior slope of the promontorium (?rostral entotympanic, fig. 16, R). It then turned abruptly to enter the basioccipital embayment that presumably contained the enlarged inferior petrosal sinus.

The area occupied by the auditory region posterior to the bulla is very small; the distance from the posterior bulla wall to the base of the paraoccipital process is only ~5–6 mm in the holotype skull. The posterior wall of the auditory region formed by the mastoid and exoccipital bones is excavated

as a shallow depression situated between the mastoid and paroccipital processes. It is bisected by the mastoid-exoccipital suture, which remains prominent in adults. The medial portion of this depressed surface is rugose and was the site of origin of the digastric muscle.

Several features of the basicranium indicate that *A. brachykolos* retained a relatively primitive arctoid auditory region: (1) the basicranium occupies only a small area of the skull in ventral view and lacks any evident anatomical specializations; (2) the bulla is a rudimentary arctoid type, formed chiefly by an ectotympanic bone, either entirely lacking, or with only a minor caudal entotympanic contribution; (3) the thin-walled, delicate construction of the bulla and the absence of bulla expansion posterior to the mastoid processes of the skull; and (4) the very small area occupied by the posterior auditory region behind the bulla anterior to the paroccipital processes. The bulla of *A. brachykolos* closely corresponds in structure and form to the auditory bulla and basicranium of *Da-*

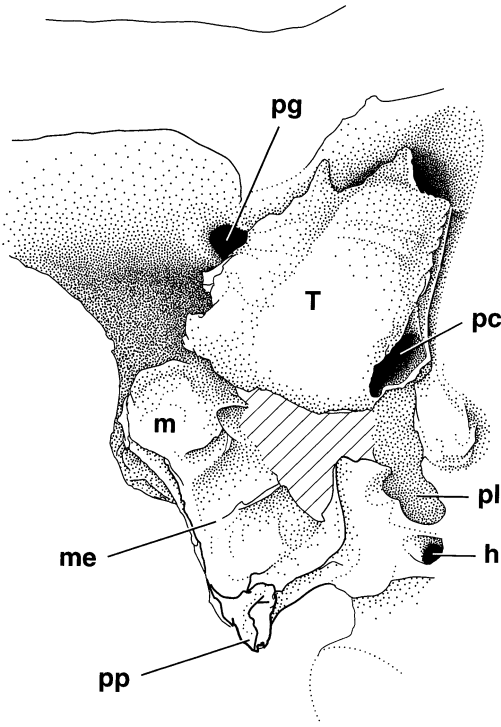


Fig. 18. Drawing of right auditory region of *Daphoenodon superbus* (anterior at top), CM 1589, holotype female, from the carnivore dens at Agate National Monument, Carnegie Quarry 3, basal Upper Harrison beds, Sioux Co., Nebraska. The auditory bullae of *D. superbus* and *A. brachykolos* (fig. 17) are similar in form and indicate a relationship between the two species.

phoenodon superbus (CM 1589), providing evidence of the close relationship of the two genera within the New World amphicyonid subfamily Daphoeninae.

Daphoenodon falkenbachi,
new species

Figures 19, 20, 21A, 23, 25A

HOLOTYPE: F:AM 54144, complete skull and associated mandibles (figs. 19, 20, 21A).

ETYMOLOGY: Named for the late C.H. Falkenbach, Frick Laboratory (AMNH), who led field parties south of Lusk, Wyoming, that discovered the holotype in 1939.

TYPE LOCALITY: 18 Mile District of C.H. Falkenbach, Goshen County, Wyoming.

TYPE HORIZON: Upper Harrison beds

(“High Brown Sand” of Falkenbach), upper Arikaree Group (early Miocene).

REFERRED SPECIMENS: Referred material is from the Upper Harrison beds in Sioux County, Nebraska, and Niobrara, Goshen, and Platte Counties, southeastern Wyoming: (1) F:AM 54146, partial left mandible with p4–m3, partial right mandible with m2, from 5 miles southeast of Chugwater, Platte County, Wyoming; (2) F:AM 54145, left partial mandible with c–m1 that makes a reliable contact with a fragment with m2 (F:AM 54150), indicating the same individual, from 5 miles southeast of Chugwater, Platte County, Wyoming; (3) CM 3719, left mandible of a young individual with m1–2, partial p4, Niobrara Canyon, Sioux County, Nebraska; (5) UNSM 99420, partial rostrum with left P1–M2, right I3, and partial postcranial skeleton, from the Lay Ranch paleovalley, west of Spoon Butte, Goshen County, Wyoming.

KNOWN DISTRIBUTION: Latest Arikareean of Sioux County, Nebraska, and Niobrara, Goshen, and Platte Counties, Wyoming.

DIAGNOSIS: Mid-sized species of the genus in the North American midcontinent; distinguished by larger size from *Daphoenodon notionastes* (~34–38%) and *D. superbus* (~10–23%), demonstrated by cranial (table 1) and dental measurements (tables 2, 3). The posterior border of p4 in *D. falkenbachi* is more rounded than in *D. superbus* and *D. notionastes* in which the posterior p4 margin is usually straight, with squared corners. Length of m2 relative to m1 length (table 4) in *D. superbus* (54.5–63.1%, N = 5) is slightly greater than in *D. falkenbachi* (51.3–54.3%, N = 3), indicating a shorter m2 in *D. falkenbachi*. Distinguished from *A. brachykolos* by a lower, wider skull with less downward rotation of the facial region on the posterior cranium and by short, broader anterior premolars. Dental formula: 3-1-4-3/3-1-4-3.

The postcranial skeleton of *D. falkenbachi* is poorly known, represented only by the partial skeleton of a single individual (UNSM 99420) collected in 1983 from the Lay Ranch beds west of Spoon Butte: included are the tibia (without distal end), distal fibula, calcaneum, proximal ulna, carpal cuneiform, scapholunar, a proximal phalanx, and a few ribs and vertebrae, which do not provide suf-



Fig. 19. Holotype cranium and mandible of *Daphoenodon falkenbachi*, F:AM 54144, Upper Harrison beds, 18 Mile District, Goshen Co., Wyoming. Scale bar, 5 cm.

ficient information to determine the degree of elongation of the lower limbs.

DISCUSSION: In the lowest stratigraphic level of the Upper Harrison beds in northwestern Nebraska, waterholes and carnivore dens have produced most of the the known sample of *Daphoenodon superbus*, the holotype species of the genus. The species was discovered and named by O.A. Peterson (1907, 1909b, 1910) for specimens from the carnivore dens of Carnegie Quarry 3 at Agate National Monument in Sioux County. In the higher stratigraphic levels of the Upper Harrison beds in northwestern Nebraska and southeastern Wyoming, *Daphoenodon* is represented by a species larger and more robust than *D. superbus*. This species is herein named *D. falkenbachi* for Charles Falkenbach of the Frick Laboratory whose field crews collected the holotype cranium and mandibles in 1939 from the 18 Mile District, northern Goshen County, Wyoming. A few additional mandibular fragments with teeth of *D. falkenbachi* were found by Frick field parties in 1939–1940 near Chugwater, Platte County, Wyoming.

Almost all specimens of *D. falkenbachi*

come from southeastern Wyoming, whereas the entire sample of *D. superbus* is from northwest Nebraska. However, the two species occur together in superposed stratigraphic relationship in the Niobrara Canyon as described below. On September 4, 1901, a mandible of *D. falkenbachi* (CM 3719), initially identified as ?*Aelurodon*, was found by O.A. Peterson along the Niobrara River in Sioux County. We know from field records of the Carnegie Museum that Peterson collected the mandible in the Niobrara Canyon, southwest of Harrison, Nebraska, in outcrops he later designated as the type area for the Upper Harrison beds (Peterson, 1909a). Sediment adhering to the mandible confirms that it was collected in the Upper Harrison beds from the pale brownish-gray volcanoclastic loess lithofacies. In the Niobrara Canyon this lithofacies always occurs stratigraphically above the waterhole bonebeds (Harper Quarry and equivalent sites) that yielded *D. superbus* in the lowest part of the formation. Thus, in the canyon the two species occur in superpositional relationship: *D. superbus* in a bonebed (Harper Quarry local fauna) in the

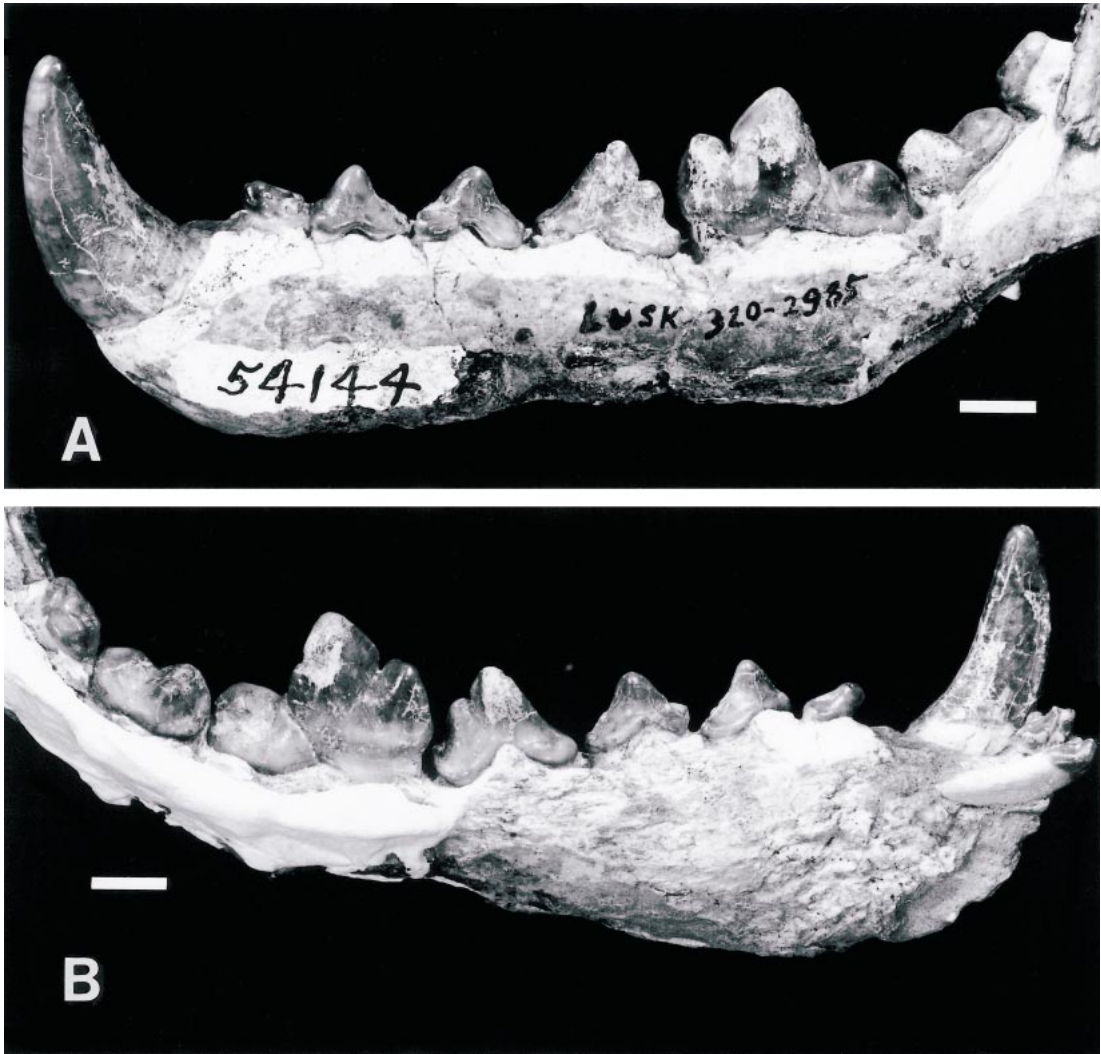


Fig. 20. Holotype left mandible of *Daphoenodon falkenbachii*, F:AM 54144, Upper Harrison beds, 18 Mile District, Goshen Co., Nebraska. **A**, lateral view; **B**, medial view. Scale bars, 1 cm.

lowest part of the formation (Hunt, 1978), and *D. falkenbachii* from a higher level within the pale brown volcanoclastic loess (Niobrara Canyon local fauna, Hunt, 1990).

Identification as *Daphoenodon* is supported by the distinctive skull form of the *D. falkenbachii* holotype (FAM 54144, fig. 2B), which is identical to the skull of *D. superbus*. Both the holotype of *D. falkenbachii* and the holotype skull of *D. superbus* (CM 1589, Peterson, 1910) are low and broad crania, with a short rostrum and moderately inflated fron-

tal region. The *D. falkenbachii* skull differs in these features from the high, laterally compressed cranium of *Adilophontes* from the same locality and stratigraphic unit (the holotype crania of *D. falkenbachii* and *A. brachykolos* are both from Falkenbach's 18 Mile District). In its dentition, *D. falkenbachii* lacks the characteristic squared posterior border of p4 seen in *D. superbus* (which occurs in all known mandibles of the species); *D. falkenbachii* also lacks the long, rectangular m2 of the *D. superbus* hypodigm. In other

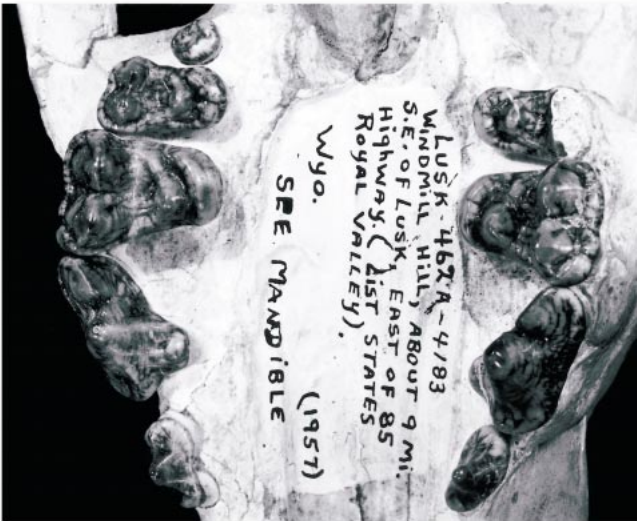
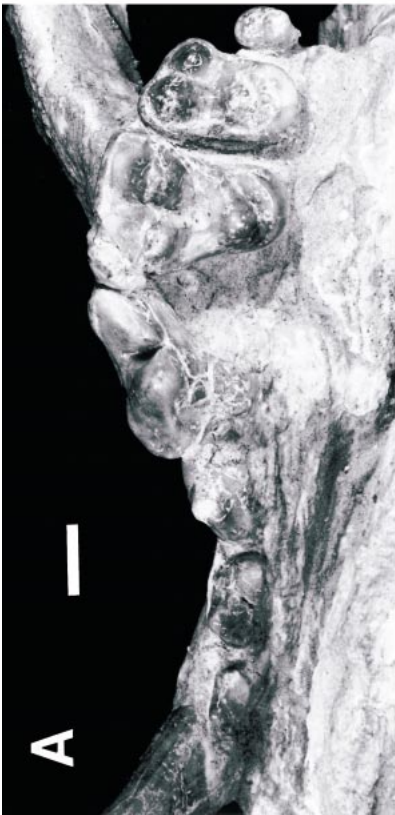


TABLE 1
Basilar Lengths of Skulls of North American Arikareean Daphoenine and Amphicyonine Amphicyonids and the European Aquitanian Amphicyonine *Cynelos*

Taxon	Museum number	Basilar length (mm)
<i>Daphoenodon superbus</i>	CM 1589, 2774, UNSM 700-82	215, 222, 243 ^a
<i>Daphoenodon notionastes</i>	UF 16910, 16997	197 ^a , 191 ^a
<i>Daphoenodon skinneri</i>	F:AM 70801	242
<i>Daphoenodon falkenbachii</i>	F:AM 54144	265
<i>Adilophontes brachykolos</i>	F:AM 27568, 54148, 54140	243, 305, 300 ^a
<i>Ysengrinia americana</i>	F:AM 54147	298
<i>Cynelos lemanensis</i>	Université de Lyon, Julien Coll.	220 ^a

^a Estimated measurement.

respects, the teeth of *D. falkenbachii* are similar in form yet larger than the teeth of *D. superbus* (tables 2, 3). *D. falkenbachii* is characterized by short yet unreduced premolars, short m2 relative to m1 length (table 4), and an m1 with a tall trigonid and a talonid with a robust, ridgelike hypoconid (fig. 20). The shorter p2 of *D. falkenbachii* differs from the longer p2 of *D. superbus*.

The absence of postcranial material for all but one individual of *D. falkenbachii* prevents a more thorough description of the skeleton. The only individual with dentition and associated postcrania is UNSM 99420 from the Lay Ranch paleovalley west of Spoon Butte, Wyoming (fig. 22). The Lay Ranch beds are equivalent in age to the Upper Harrison beds of northwest Nebraska and contain a fauna correlative with the Niobrara Canyon local fauna (Hunt, 1985a, 1990). The UNSM field party realized at the time of its discovery in 1983 that UNSM 99420 represented the only known instance of postcranial material in association with a dentition of this species. Consequently, the outcrop was thoroughly searched but very few limb elements were preserved: a partial tibia lacking the distal end, a fibula without its proximal end, a calcaneum, scapholunar, carpal cuneiform, proximal ulna, a phalanx, and a badly weathered scapula. The skeleton lacked complete limb elements (radius, ulna, metapodials) that would conclusively establish the

length of the forelimb and feet, thus allowing a comparison with the short forelimb of *A. brachykolos*. Despite these limitations, the postcrania of UNSM 99420 indicate a larger carnivore than any known individual of *D. superbus*. The limbs of *D. superbus* are not elongated in the epipodial segments, indicating a short-legged carnivore (Peterson, 1910).

Additional information on forelimb length of *D. falkenbachii* is provided by the scapholunar. Both *D. superbus* and *D. falkenbachii* (UNSM 99420) have a scapholunar of similar dorsoventral thickness. Undescribed amphicyonids closely related to *Daphoenodon* from younger Miocene rock units in the UNSM collection have elongate forelimbs associated with much thicker scapholunars, suggesting that the elongation of the forelimb is correlated with an increase in thickness of this carpal bone. The scapholunar of UNSM 99420 does not show this increase in thickness, suggesting that the forelimb was not significantly lengthened.

The basicranium is preserved only in the holotype (fig. 23), and its structure is like that of the basicranium of *D. superbus* (CM 1589). Although damaged by crushing, the right petrosal and left auditory bulla are preserved. The bulla (fig. 23A) has the characteristic asymmetric flask-shaped form of the bullae of *D. superbus* and *A. brachykolos* in which the anterior part has been extended or

←

Fig. 21. **A**, upper dentition of holotype cranium, *Daphoenodon falkenbachii*, F:AM 54144, 18 Mile District, Goshen Co., Wyoming; **B**, upper dentition of holotype cranium, *D. skinneri*, F:AM 70801, ~9 miles (14.5 km) southeast of Lusk, Niobrara Co., Wyoming. Stereophotographs. Scale bars, 1 cm.

TABLE 2
Dental Measurements (length \times width in mm) of Lower Teeth of North American Arikareean Species of
Adilophontes and *Daphoenodon*

	p2	p3	p4	m1	m2	c-m2	p1-4
<i>Daphoenodon superbus</i>							
CM 1589	10.3 \times 5.2	12.8 \times 5.8	16.2 \times 7.9	24.2 \times 11.6	13.9 \times 9.8	92.0	47.7
CM 1589a	(12.7) ^a	(12.7)	18.6 \times 8.8	26.2 \times 11.4	(15.7)	(87.5)	(45.7)
CM 1589b	(12.8)	—	—	—	—	—	—
CM 1589b	—	14.8 \times 6.8	—	—	—	—	—
CM 1589b	—	—	—	—	—	17.4 \times 11.5	—
CM 1589b	—	—	—	—	—	14.6 \times 10.4	—
CM 1589d	—	—	—	25.9 \times 11.6	—	—	—
CM 1896g	12.2 \times 5.8	—	—	—	—	—	—
CM 2774	11.3 \times 5.5	13.6 \times 6.1	17.2 \times 8.6	24.2 \times 11.1	14.2 \times 9.8	92.5	51.0
CM 2217	—	—	—	26.1 \times 11.5	—	—	—
AMNH 81003	12.4 \times 5.9	14.3 \times 6.7	18.1 \times 9.5	25.2 \times 11.3	15.9 \times 10.1	102.7	57.4
AMNH 81025	(12.9)	(14.4)	18.7 \times 9.8	27.4 \times 11.7	(14.9)	—	—
AMNH 81055a	11.0 \times 5.6	13.3 \times 6.1	17.1 \times 8.3	—	—	—	—
AMNH 81055b	11.7 \times 5.6	14.2 \times 6.5	—	—	—	—	—
AMNH 81052	—	—	—	24.9 \times 11.2	—	—	—
FMNH P12033	11.1 \times 5.5	12.4 \times 5.9	16.5 \times 7.8	26.1 \times 11.8	(15.2)	(93.4)	49.2
F:AM 54460	12.2 \times 6.1	13.5 \times 7.4	18.7 \times 9.1	24.7 \times 12.0	14.0 \times 10.6	94.6	53.3
UNSM 44683	—	—	—	25.8 \times 11.4	—	—	—
UNSM 44688	12.3 \times 6.0	—	18.0 \times 9.1	25.3 \times 11.7	15.7 \times 10.8	95.5	51.6
UNSM 700-82	12.6 \times 5.6	13.6 \times 6.4	19.3 \times 8.9	26.4 \times 11.6	15.2 \times 10.1	104.9	(60)
<i>Daphoenodon notionastes</i>							
UF 16965	—	—	—	21.8 \times 10.6	—	—	—
UF FGS-V1213	—	—	—	21.6 \times 9.7	—	—	—
UF 449	—	—	—	19.3 \times 9.4	—	—	—
UF 16905	—	—	—	—	12.3 \times 8.7	—	—
UF 16968	—	—	15.6 \times 6.8	—	—	—	—
UF 16970	—	—	14.9 \times 6.0	—	—	—	—
LSUMG-V2256	—	—	20.8 \times 10.3	10.3 \times 7.7	—	—	—
UF 16997	(11.2 \times 4.5)	(12.6 \times 5)	(16.1 \times 6.4)	(19.6 \times 7.9)	(10.1 \times 5.7)	(80.4)	(48.4)
UF 16910	(12.0 \times 5.1)	(13.3 \times 5.5)	(15.7 \times 6.6)	(21.4 \times 8.5)	(12.2 \times 6.6)	(81.3)	(46.9)
<i>Daphoenodon falkenbachi</i> , n. sp.							
F:AM 54144	13.1 \times 7.3	14.8 \times 7.4	19.3 \times 9.7	30.2 \times 13.5	16.4 \times 11.5	104.5	56.7
F:AM 54145/ 54150	(11.9)	(15)	(19.3)	28.9	(16.1)	(98)	53.5
CM 3719	—	—	(19.6) \times 10.3	30.8 \times 14.1	15.8 \times 10.6	(99)	(51)
F:AM 54146	—	—	17.8 \times 9.1	\times 12.0	16.3 \times 11.1	—	—
<i>Daphoenodon skinneri</i> , n. sp.							
F:AM 70801	11.3 \times 6.2	13.2 \times 7.0	16.8 \times 9.1	26.0 \times 12.2	14.0 \times 10.4	93.5	53.2
<i>Adilophontes brachykolos</i> , n. gen., n. sp.							
F:AM 27568	14.6 \times 7.0	16.1 \times 7.8	(18.0 \times 10.7)	(29 \times 13.9)	16.4 \times 11.0	106.5	58.3
F:AM 54148	13.7 \times 7.1	16.0 \times 8.2	20.7 \times 10.8	28.5 \times 14.1	16.5 \times 13.3	111.6	58.4
F:AM 54141	13.1 \times 6.7	—	—	(29) \times 13.6	16.5 \times 12.1	(100)	—

^a () Indicates estimated measurement.

inflated, entirely filling the anteromedial auditory region. A short bony external auditory meatus of 6–7 mm length was present. The posterior wall of the bulla was thin, trans-

versely oriented, and uninflated; its position shows that the bulla did not extend behind the mastoid processes.

The middle ear cavity was ~19.5 cm in

TABLE 3
Dental Measurements (length \times width in mm) of Upper Teeth of North American Arikareean Species of *Adilophontes* and *Daphoenodon*

	P2	P3	P4	M1	M2	C-M2	P1-4
<i>Daphoenodon superbis</i>							
CM 1589	11.5 \times 5.3	13.1 \times 7.1	22.3 \times 13.7	18.6 \times 23.5	12.6 \times 19.1	84.6	55.1
CM 1589a	12.3 \times 5.7	14.1 \times 7.2	25.1 \times 15.0	18.7 \times 24.3	13.6 \times 19.4	83.1	56.8 ^a
CM 1589b	—	16.3 \times 8.8	\times 14.9	—	12.8 \times 19.6 ^b	—	—
CM 1589b	—	—	—	—	13.6 \times 20.8	—	—
CM 2774	11.1 \times 5.2	(12.5) ^c \times 6.4	22.8 \times 13.9	17.8 \times 23.8	12.3 \times 19.0	80.6	52.4
AMNH 81055	11.7 \times 5.0	—	22.3	17.9 \times 22.5	11.3 \times 17.9	—	—
AMNH 81046	—	—	—	19.9 \times 24.5	—	—	—
AMNH 81048	—	—	—	18.6 \times 24.3	—	—	—
AMNH 81050	—	—	—	17.0 \times 21.1	—	—	—
AMNH 83484	—	—	23.2 \times 13.8	—	—	—	—
<i>Daphoenodon notionastes</i>							
UF 449	—	—	—	16.5 \times 19.1	—	—	—
UF 16906	—	—	20.3 \times 11.7	—	—	—	—
<i>Daphoenodon falckenbachi</i> , n. sp.							
F:AM 54144	13.7 \times 7.5	15.8 \times 8.9	27.1 \times 18.8	22.1 \times 26.9	15.0 \times 21.7	96.1	67.6
UNSM 99420	13.0 \times 6.5	16.1 \times 8.0	26.4 \times 16.2	22.0 \times 27.7	14.3 \times 21.6	101.2	70.5
<i>Daphoenodon skinneri</i> , n. sp.							
F:AM 70801	12.0 \times 6.1	13.8 \times 7.5	24.0 \times 14.0	17.9 \times 22.9	11.4 \times 18.5	83.9	62.4
<i>Adilophontes brachykolos</i> , n. gen., n. sp.							
F:AM 54148	13.6 \times 7.5	19.5 \times 9.4	27.4 \times 17.6	22.0 \times 27.7	15.1 \times 23.0	108.1	75.3
F:AM 27568	13.9 \times 7.0	16.5 \times 7.9	26.0 \times 15.2	21.3 \times 24.0	13.0 \times 20.0	93.3	66.4
F:AM 54140	13.2 \times 7.0	17.2 \times 8.4	27.5 \times 17.9	21.1 \times 27.7	13.7 \times 22.1	103.8	74.5

^a Juvenile with *en echelon* premolars.

^b The teeth of CM 1589b are not necessarily from a single individual but are from the carnivore den site (Carnegie Museum Quarry 3) at Agate National Monument and so are sampled from a single population.

^c () Indicates estimated measurement.

length and perhaps ~ 13 mm in maximum width. The cavity extended ventral to the tympanum a short distance into the floor of the bony external auditory meatus, creating a bony shelf 5.5 mm in width ventral to the crista tympani; anterior to this shelf is a small pocket in the anterolateral wall of the bulla similar to this same feature in the holotype of *A. brachykolos*. The paroccipital processes, although damaged, were relatively larger and more posteriorly directed than in *A. brachykolos* and were similar in these respects to *D. superbis*.

A bony tube for the internal carotid artery is present within the medial bulla wall which is applied to the medial margin of the right petrosal promontorium. The tube begins at the posteromedial corner of the bulla and ap-

parently took the same path as in *A. brachykolos*. The lateral margin of the basioccipital was embayed for the enlarged inferior petrosal venous sinus.

A low, rounded promontorium is typical of the petrosals of *D. falckenbachi*, *D. superbis*, and *A. brachykolos*. However, in *Adilophontes* the promontorium is somewhat longer and wider than in *Daphoenodon*, relative to overall skull size. The characteristic depressions (tensor tympani fossa, epitympanic recess, stapedius fossa) in the ventral surface of the tegmen tympani in both genera are simple and without specializations, and the tensor fossa and epitympanic recess are confluent without a ridge separating them. The similarities in bulla and petrosal morphology support a relationship between *Da-*

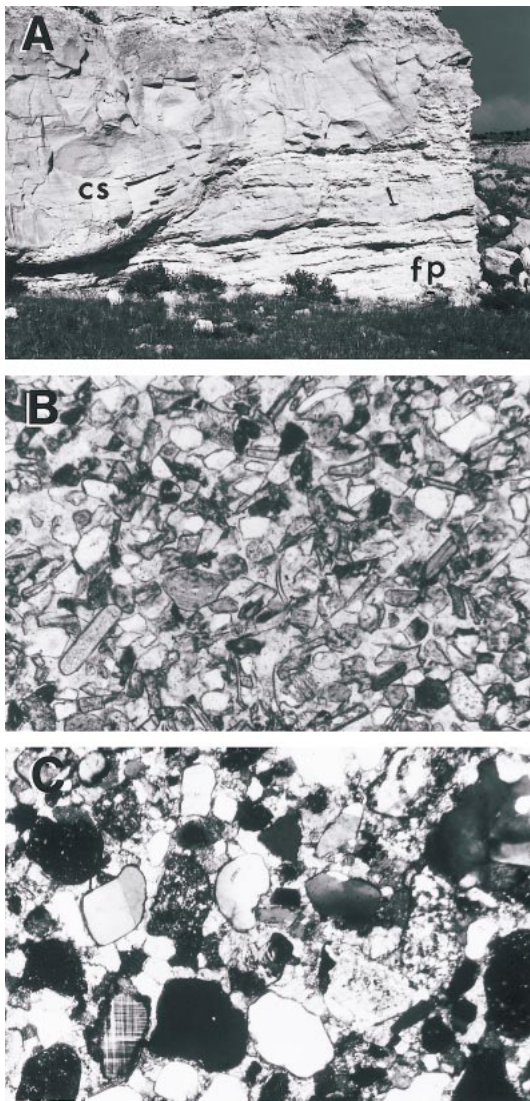


Fig. 22. Fluvial lithofacies of the Lay Ranch beds, a latest Arikareean paleovalley at Spoon Butte, Goshen Co., Wyoming, that produced the amphicyonids *A. brachykolos*, *D. falkenbachii*, and *Ysengrinia*: **A**, channel (cs) and floodplain (fp) facies within the Lay Ranch paleovalley (*D. falkenbachii*, UNSM 99420, was found in interbedded floodplain silts and fine sands ~100 m northeast of this outcrop)—hammer on outcrop, 30 cm length; **B**, photomicrograph of tuffaceous very fine sand (glass shards, 41%) from the Lay Ranch paleovalley floodplain that includes both reworked airfall ash and a minor epiclastic fraction derived from the Hartville Uplift to the west; **C**, photomicrograph of cross-stratified epiclastic sandstone derived from the Precambrian core of the Hartville Uplift; this lithofacies rarely occurs

TABLE 4
Ratio of m2/m1 Length in Species of North American *Daphoenodon* and *Adilophontes*

<i>Daphoenodon notionastes</i>	
UF 16905/16965 ^a	0.56
LSUMG-V2256	0.50
UF 16910	0.57 ^b
UF 16997	0.52 ^b
<i>Daphoenodon superbus</i>	
CM 1589	0.57
CM 1589a	0.60 ^b
CM 2774	0.59
AMNH 81003	0.63
FMNH P12033	0.58
F:AM 54460	0.57
UNSM 44688	0.62
UNSM 700-82	0.58
<i>Daphoenodon skinneri</i> , n. sp.	
F:AM 70801	0.54
<i>Daphoenodon falkenbachii</i> , n.sp.	
F:AM 54144	0.54
F:AM 54145/54150	0.56 ^b
CM 3719	0.51
<i>Adilophontes brachykolos</i> , n. gen., n. sp.	
F:AM 27568	0.57 ^b
F:AM 54148	0.58
F:AM 54141	0.57 ^b

^a m1-m2 not associated but are from the Buda local fauna (Arikareean), Florida.
^b Indicates ratio based on estimated measurement(s).

phoenodon and *Adilophontes* within the sub-family Daphoeninae.
A skull with associated mandibles (F:AM 70801) from 9 miles (14.5 km) southeast of Lusk, Wyoming, represents a stratigraphically older member of the *D. falkenbachii* lineage (figs. 21B, 24). This is a smaller carnivore than *D. falkenbachii*; in all aspects of the skull, mandibles, and teeth it is clearly the predecessor to that species.

Daphoenodon skinneri,
new species
Figures 21B, 24

HOLOTYPE: F:AM 70801, a crushed skull with complete dentition (left I1–3, C, P1–

←
within the Lay Ranch paleovalley which is almost entirely filled by fluvially reworked tuffaceous eolian sediments in channels and floodplain.

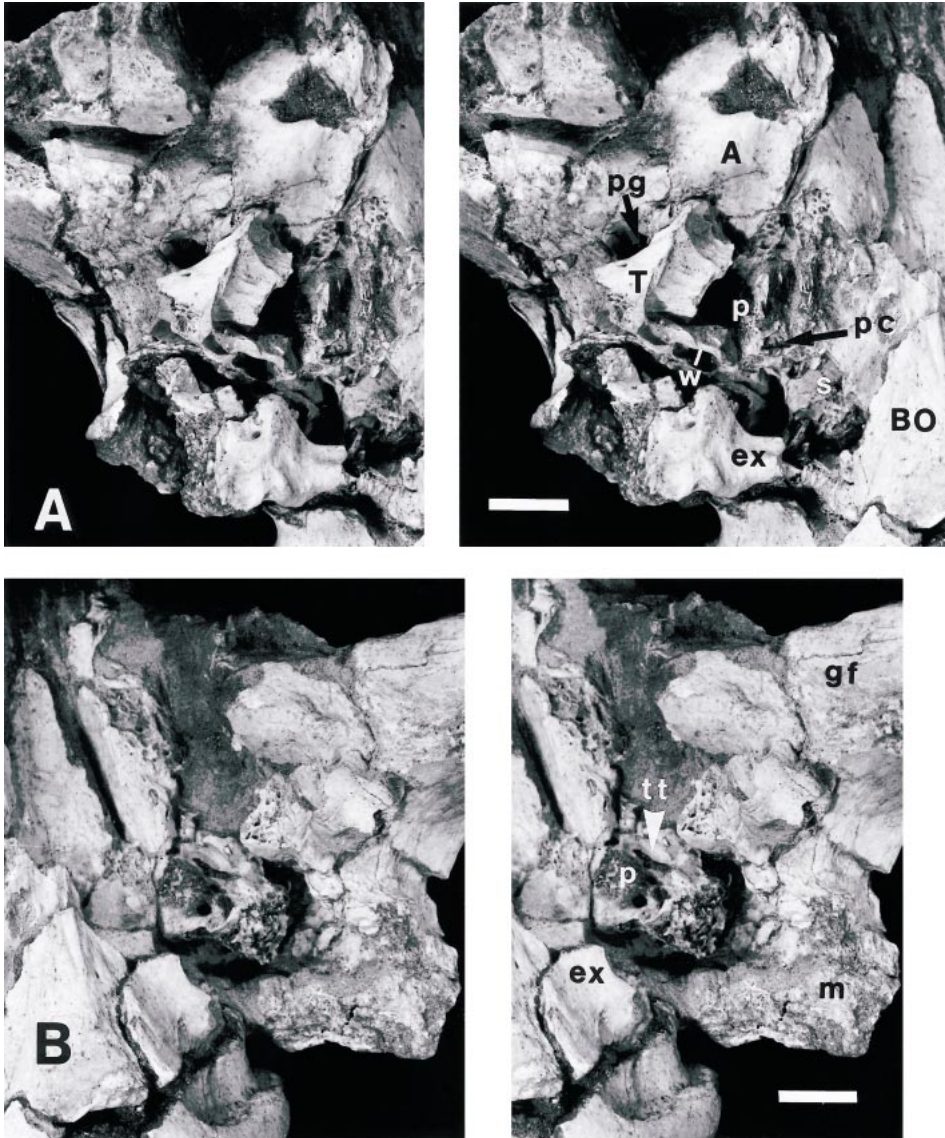


Fig. 23. Basicranium of *Daphoenodon falkenbachii*, holotype (F:AM 54144): **A**, ventral view of right auditory region showing the ectotympanic bulla; **B**, ventral view of crushed left auditory region showing the form of the petrosal. Stereophotographs. Scale bars, 1 cm.

M3, right I1–3, C, P1–M2) and associated mandibles (right and left i1–3, c, p1–m3).

ETYMOLOGY: Named for the late Morris F. Skinner, Frick Laboratory (AMNH), in recognition of his extensive contributions to the study of the geology and paleontology of western Nebraska and southeastern Wyoming.

TYPE LOCALITY: About 9 miles (14.5 km) southeast of Lusk, Royal Valley District of the Frick Laboratory (AMNH), collected somewhere within sections 25–28, 33–36, T31N, R63W, east of U.S. Highway 85, Niobrara County, Wyoming.

TYPE HORIZON: Upper Harrison beds, upper Arikaree Group (early Miocene).

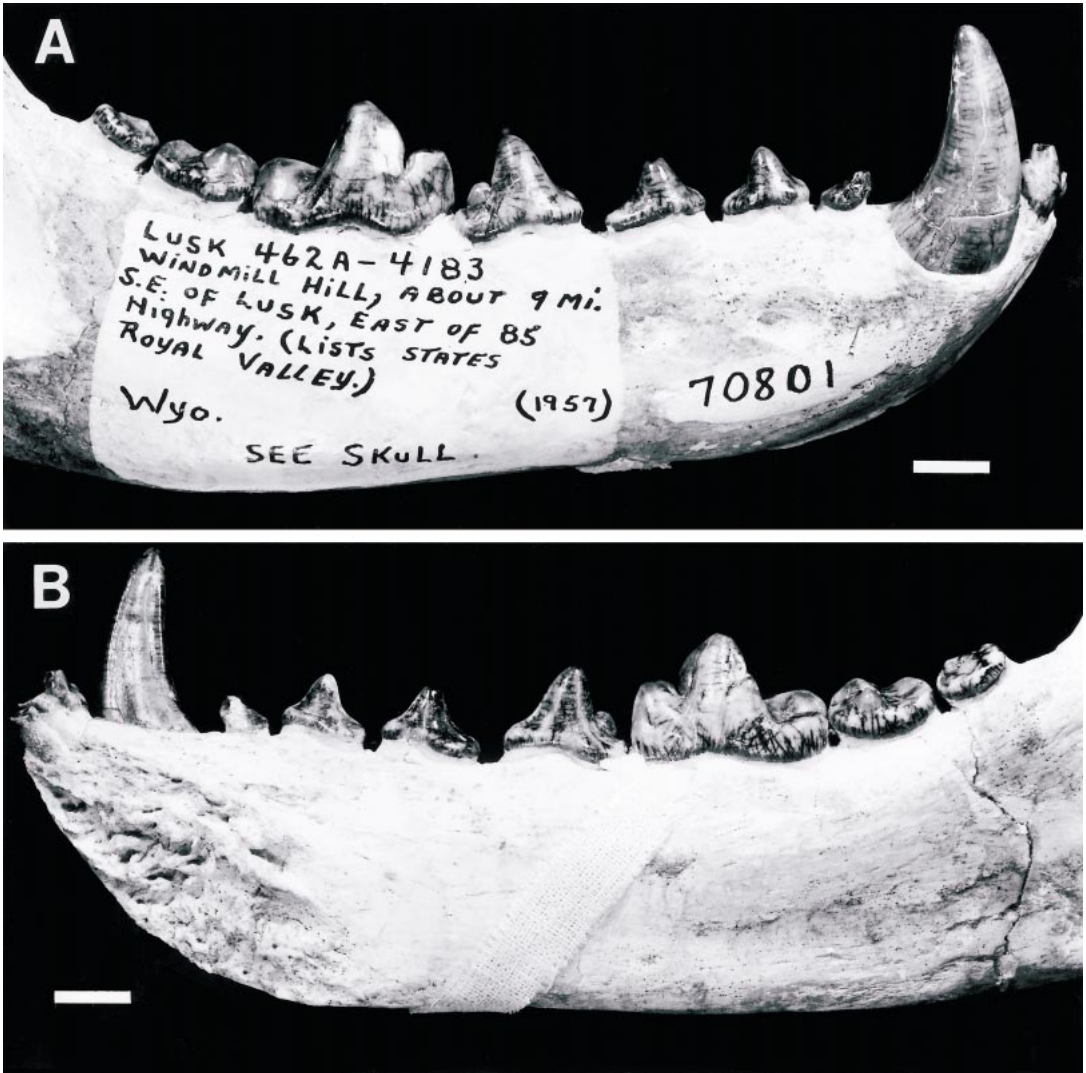


Fig. 24. Holotype right mandible of *Daphoenodon skinneri*, F:AM 70801, from ~9 miles (14.5 km) southeast of Lusk, Niobrara County, Wyoming: **A**, lateral view; **B**, medial view. Scale bars, 1 cm.

REFERRED SPECIMENS: None.

KNOWN DISTRIBUTION: Latest Arikareean, Niobrara County, Wyoming.

DIAGNOSIS: A species of the *Daphoenodon* group, closely similar in cranial and dental morphology to *D. falkenbachi*, but markedly smaller. The species is distinguished from *D. falkenbachi* by smaller size (tables 1–3), and from *D. superbis* by smaller M1–2 and m2 relative to the size of the carnassials (P4, m1). *D. skinneri* differs in the length of its

m2, which is proportionately shorter, relative to m1 length, than in *D. superbis* from northwest Nebraska (table 4). The ratio of m2 length/m1 length for *D. skinneri* is 0.54 ($N = 1$); for *D. superbis*, 0.57–0.63 ($N = 8$); for *D. falkenbachi*, 0.51–0.56 ($N = 3$); and for *A. brachykolos*, 0.57–0.58 ($N = 3$).

DISCUSSION: Although the skull of the holotype is crushed, it is apparent that the skull form is like that of *D. falkenbachi* and *D. superbis*. Its skull form differs conspicuous-

ly, however, from the deeper, more laterally compressed skull of *A. brachykolos*. When compared with the skull and mandible of the *D. superbus* holotype (CM 1589), the holotype of *D. skinneri* has proportionately smaller M1–2 and m2 but slightly larger incisors, canines, premolars, and m1.

The skull of *D. skinneri* (basilar length, 24.5 cm) is also noticeably larger than the *D. superbus* holotype (basilar length, 21.5 cm) from the Carnegie Quarry 3 carnivore dens, but this latter skull is undoubtedly female (Hunt et al., 1983); males of *D. superbus* from Quarry 3 attained the size of *D. skinneri* (table 1). However, a male *D. superbus* (UNSM 700–82) from the same den system as the *D. superbus* holotype female has canines, premolars, and molars of larger size than *D. skinneri*, and the premolars (p2–4) of UNSM 700–82 are much longer and narrower than those of *D. skinneri* (table 2), demonstrating that *D. skinneri* is not simply a male of *D. superbus*. *D. superbus* and its close relative, *D. notionastes*, are characterized by longer and more slender premolars relative to the shorter, wider premolars of *D. skinneri* and its descendant *D. falkenbachii*.

No postcranials were found with the holotype of *D. skinneri*.

The site where the holotype of *D. skinneri* was collected can be approximately located (fig. 1). Records of the Frick Laboratory (AMNH) state that the specimen was obtained in 1957 from the private collection of N.Z. Ward, a member of Falkenbach's field crew. Falkenbach and Ward worked together in Upper Harrison beds south of Lusk in southern Niobrara County in 1961–1962, but not in 1957. Apparently Ward found the skull in 1957 during his own exploration of Upper Harrison exposures in southern Niobrara County. The locality marked on F:AM 70801 reads "about 9 mi S.E. of Lusk" which was included in the Royal Valley District (letter from C.H. Falkenbach to Childs Frick, June 18, 1942). The Royal Valley District includes Upper Harrison outcrops at Royal Valley (west of Highway 85) that are situated 3–4 miles (4.8–6.4 km) west of similar outcrops ~9 miles (14.5 km) southeast of Lusk (east of Highway 85). Outcrops in these two localities occur in the S½, T31N, R63W, and appear to represent the same lithic unit, a

western facies of the Upper Harrison beds developed in southern Niobrara County. The sediment remaining on the skull is a light gray very fine sandstone typical of Upper Harrison sediments exposed today at Royal Valley and 9 miles (14.5 km) southeast of Lusk. These exposures apparently carry a fauna somewhat older than the Upper Harrison beds to the south in the 18 Mile District of C.H. Falkenbach that yielded fossils of the larger and more advanced *D. falkenbachii*.

DISCUSSION

Dental dimensions and tooth morphology, but particularly the distinctive form of the skull, most clearly distinguish these species of amphicyonids. The shorter premolars of *Daphoenodon falkenbachii* and *D. skinneri* contrast with the more elongate and narrow premolars of *A. brachykolos* (fig. 25). Similarly, a bivariate plot of the dimensions of the lower carnassial and the m2 of these bearded dogs differentiates *D. falkenbachii*, *D. skinneri*, *D. superbus*, and *D. notionastes* from *Adilophontes* (fig. 26). Dimensions of the upper carnassial and molars also contribute to discrimination among these species (fig. 27). These bivariate plots show that *A. brachykolos* and *D. falkenbachii* display the largest carnassials and molars. However, while these two species have consistently larger carnassials and upper molars (M1–2) relative to *D. superbus* and *D. notionastes*, their m2 dimensions are much closer to *D. superbus*, reflecting a failure to significantly lengthen m2 in *D. falkenbachii* and *A. brachykolos*. Based on dental measurements, the series *Daphoenodon notionastes-superbus-skinneri-falkenbachii* shows a progressive increase in tooth size that accompanies larger body size in this genus.

Amphicyonids from the Upper Harrison beds of southeastern Wyoming and contiguous outcrops in northwest Nebraska comprise a unique assemblage of large carnivores that is restricted to the formation and does not occur in younger faunas of the central Great Plains (fig. 28). Amphicyonids from the lowest levels of the Upper Harrison in northwest Nebraska include *Daphoenodon superbus* (the common indicator taxon, confined to this stratigraphic level) and the am-

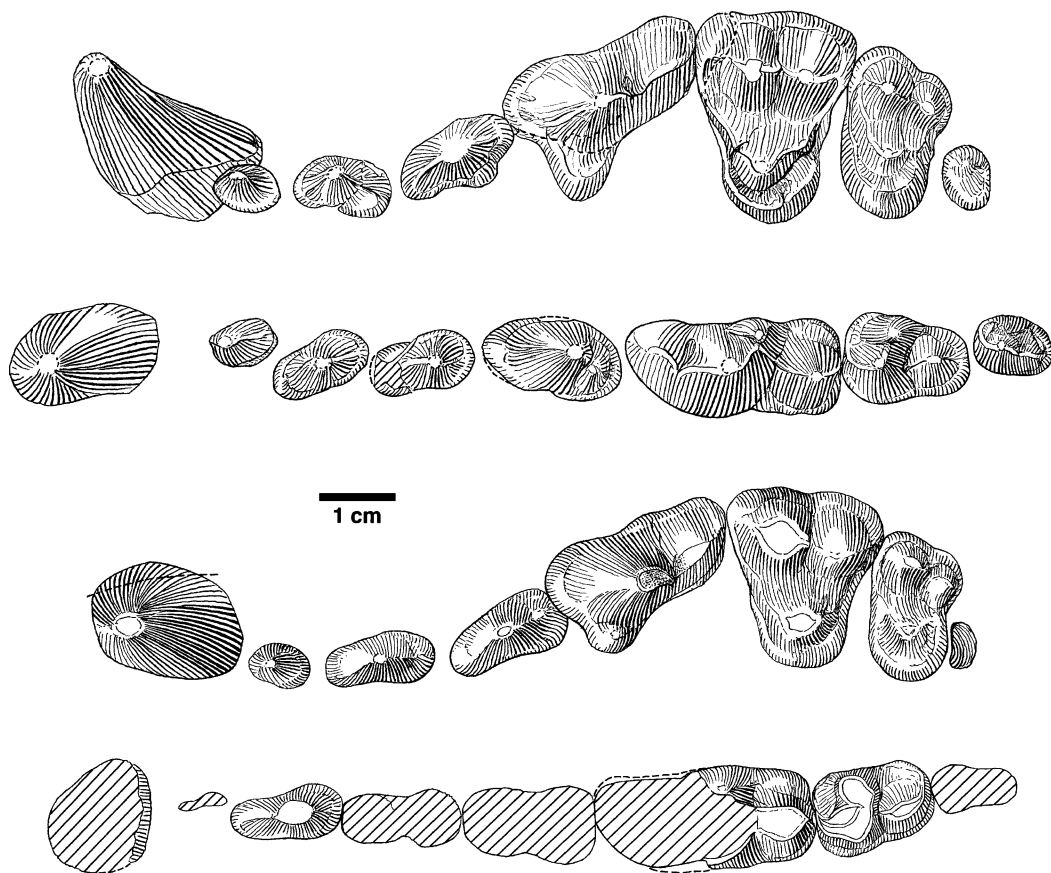


Fig. 25. Comparison of upper and lower dentitions of *Daphoenodon falkenbachi* (**above**), holotype, F:AM 54144, and *Adilophontes brachykolos* (**below**), holotype, F:AM 27568, both from the Upper Harrison beds, 18 Mile District, Goshen County, Wyoming. Note the difference in form of the premolars. Scale bar 1 cm.

phicyonines *Ysengrinia americana* (Hunt, in press a) and rare remains of *Cynelos*. These carnivorans come from stream and waterhole deposits of the basal Upper Harrison at Agate National Monument and in the Niobrara Canyon (Hunt, 1990). Higher stratigraphic levels of the Upper Harrison have produced the more advanced *D. falkenbachi*, as well as *Y. americana* and *A. brachykolos*. However, outcrops in southernmost Niobrara County that yielded *D. skinneri* appear to carry a slightly older fauna than typical Upper Harrison exposures with *D. falkenbachi* in Goshen County. In Goshen County an apparently homogeneous Upper Harrison mammalian fauna comes from the collecting districts of Falkenbach south of Lusk,

Wyoming, and from the Lay Ranch beds at Spoon Butte; a time-equivalent fauna is derived from outcrops along the western margin of Goshen Hole in southeastern Platte County, Wyoming.

The stratigraphically superposed faunas of the early Hemingfordian Runningwater Formation in northwest Nebraska lack these earlier species of *Daphoenodon*, *Ysengrinia*, and *Cynelos*, and instead contain the first New World appearances of the immigrant Eurasian amphicyonine *Amphicyon* (Hunt, in press b), a new larger species of *Cynelos*, and a very large digitigrade species of daphoenine amphicyonid with elongate limbs and feet, *Borocyon* Peterson 1910 (Hunt, in prep.). The shift in the amphicyonid taxa

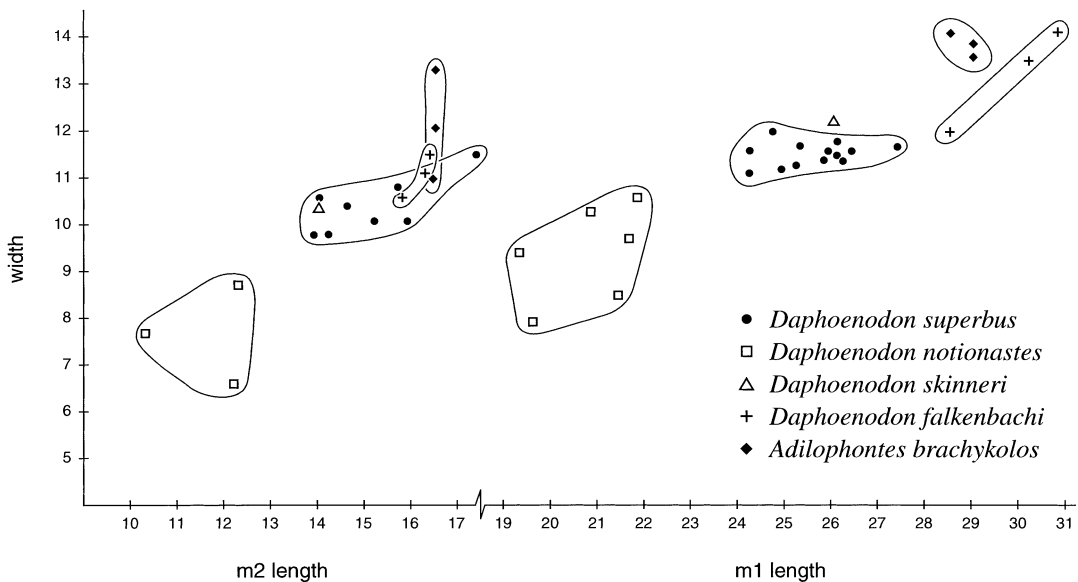


Fig. 26. Dimensions (in mm) of the lower molars (m1, m2) of the amphicyonids *Adilophontes* and *Daphoenodon*. *A. brachykolos* and *D. falckenbachi* have a short m2 relative to m1 length when compared to *D. superbus*. The sample of *Daphoenodon superbus* (N = 13) demonstrates the extent of variation in these measurements in a single species from a limited stratigraphic interval.

from the Upper Harrison into the Runningwater is part of a highly selective faunal transformation at the beginning of the Hemingfordian NALMA in the Great Plains of North America.

Among the large carnivorans that have their last appearances in the Upper Harrison fauna of southeastern Wyoming and northwest Nebraska are the amphicyonids *Y. americana*, *D. skinneri*, *D. falckenbachi*, *D. superbus*, and the giant mustelid *Megalictis ferox*. Several lineages of temnocyonine amphicyonids that persisted throughout the Arikarean also did not extend into the early Hemingfordian. Upper Harrison horses paralleled the carnivorans in last appearances of *Parahippus wyomingensis* and the very large *P. nebrascensis*. These equids were replaced in the early Hemingfordian by *Parahippus tyleri*, *P. pawniensis*, and *Archaeohippus*. On the other hand, a number of oreodonts, camels, peccaries, the entelodont *Dinohyus*, and ruminant artiodactyls ranged from the Upper Harrison into the Runningwater fauna: *Merychys* evolved from a smaller into a larger species; the large *Merycochoerus matthewi* evolved directly into *M. magnus* and *M. pro-*

prius; and several lineages of small moschid and dromomerycid deer persisted as well (Webb, 1998). Stenomyline camels, *Oxydactylus*, and the protolabines *Michenia*, *Protolabis*, and *Tanymycter* also survived the Upper Harrison–Runningwater faunal transition (Honey et al., 1998), as did diceratherine rhinoceroses, the long-footed rhinoceros *Menoceras*, tapirs, and chalicotheres. The hypertragulids made their last appearance in the Upper Harrison as the genus *Nanotragulus*, possibly replaced by the first occurrence of merycodont antilocaprids in the Runningwater Formation.

The last occurrences of a number of mammal species in the Upper Harrison and the appearance of new mammals in the Runningwater fauna are in part explained by the depositional environments represented in each of these formations (Hunt, 1985b). Most Upper Harrison rocks belong to the volcanoclastic loess lithofacies (fig. 4), and represent episodic accumulations of fine-grained eolian tuffaceous sediment settling on open semiarid grassland plains east of the Hartville and Laramie uplifts (Hunt, 1990). On the other hand, a significant proportion

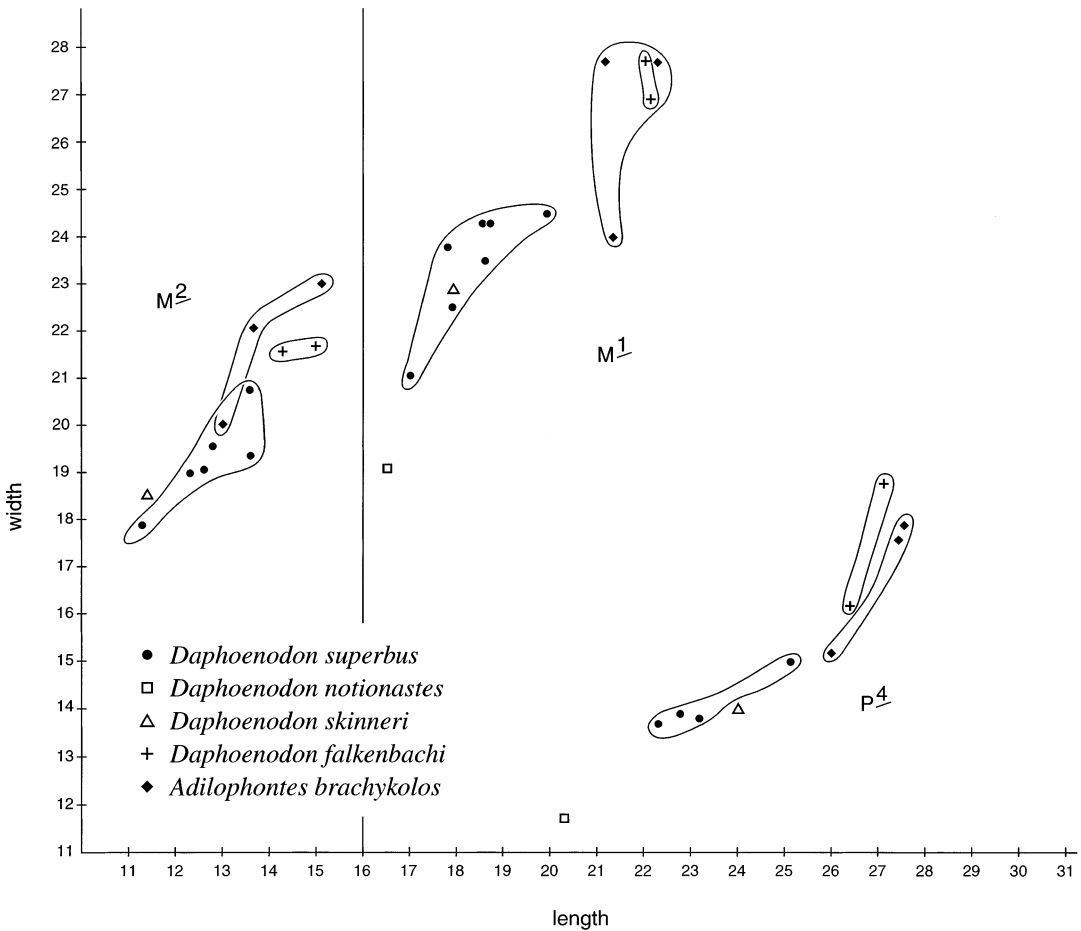


Fig. 27. Dimensions (in mm) of the upper cheek teeth (P4, M1, M2) of the amphicyonids *Adilophontes* and *Daphoenodon*. *A. brachykolos* and *D. falkenbachii* are larger carnivores relative to *D. superbus* and *D. notionastes*, reflected in their larger carnassials and upper molars.

of Runningwater exposures represent fluvial facies deposited in channels and floodplains of a major throughgoing river system draining the northern Laramie Mountains and Hartville Uplift and carrying granitic pebble gravels derived from Precambrian rocks of the Laramie Mountains (Skinner et al., 1977; Yatkola, 1978; Hunt, 1985a). Such a major drainage has not been discovered in the Upper Harrison beds of southeastern Wyoming or the western panhandle of Nebraska. The most prominent Upper Harrison paleovalley occurs in the vicinity of Spoon Butte in Goshen County (fig. 22); there the Lay Ranch beds comprise fine-grained tuffaceous silts and sands representing fluvially reworked

Arikaree air-fall sediment—lenses of granitic sands derived locally from the Hartville Uplift to the west are extremely rare and found in only a few localities (Hunt, 1990).

Thus, mammals restricted to, or commonly frequenting riparian settings near, a master stream of Runningwater type are absent from the Upper Harrison faunas. The “sudden” appearance in the Runningwater faunas of numerous small carnivores (leptartine and musteline mustelids, the lutrine mustelid *Mionictis*, paleomustelid *Brachypsalis*, the semiaquatic *Potamotherium*, and procyonid *Edaphocyon*) previously unknown in the Great Plains, together with the advent of new insectivores and rodents, and the frequent oc-

Ma	NALMA	Lithic Unit	SE Wyoming	Western Nebraska
17.5	Early Hemingfordian	Runningwater Formation		<i>Borocyon robustum</i> <i>Amphicyon galushai</i> *
18.8				<i>Borocyon robustum</i> <i>Amphicyon galushai</i> * <i>Cynelos</i> sp. <i>B</i>
19.2	Latest Arikareean	Upper Harrison Beds	<i>Daphoenodon falkenbachii</i> <i>Ysengrinia</i> sp. <i>Adilophontes brachykolos</i>	<i>Daphoenodon falkenbachii</i> <i>Ysengrinia</i> sp.
			<i>Daphoenodon skinneri</i>	
				<i>Ysengrinia</i> sp. <i>Daphoenodon superbus</i> <i>Cynelos</i> sp. <i>A</i>
	23.0	Late Arikareean		
Harrison Formation			<i>Daphoenodon</i> sp.	<i>Ysengrinia</i> sp.

Fig. 28. Stratigraphic distribution of daphoenine and amphicyonine amphicyonids in southeastern Wyoming and western Nebraska in the early Miocene. **Amphicyon galushai*: Hunt, in press b, Bulletin of the American Museum of Natural History.

currences of anthracotheres, tapirs, alligators, and fish, coincides with the arrival of significant fluvial environments of the Runningwater Formation in the region. Sediments of large throughgoing fluvial systems are infrequently represented by surface exposures of Arikaree rocks in the region. The contrasting styles of sedimentation indicated by Upper Harrison and Runningwater rocks suggest that a number of first and last appearances are probably correlated with environmental preferences of these mammals, and do not actually reflect their “extinction” or “sudden” origin in the North American midcontinent. As such, the evident turnover in amphicyonid species at the Arikareean–Hemingfordian boundary may be at least influenced, and possibly determined, by the shift in depositional environments taking place at this time in the central Great Plains.

ANDERSON RANCH FORMATION: A NEW TERM FOR THE UPPER HARRISON

The Anderson Ranch Formation is herein proposed as a formal formation-rank term based on the stratotype of O.A. Peterson’s Upper Harrison beds in Sioux County, northwest Nebraska (Peterson, 1909a). Peterson (1909a: 75) designated prominent exposures along the Niobrara River immediately east of the Wyoming–Nebraska state boundary as the type area of the Upper Harrison beds (fig. 3). Here the river cuts a deep canyon through rocks of the upper Arikaree Group. The south wall of the Niobrara Canyon comprises laterally continuous cliff-forming outcrops that extend from the state line ~4 miles (6.4 km) to the east (Hunt, 1985b: figs. 3, 9, 10, S½, T31N, R57W). Whereas these laterally

continuous exposures could serve as the type section, it is useful to designate the thickest interval of these beds along the south wall of the canyon as the stratotype ($S\frac{1}{2}$, SE4, sec. 28, continuing into $N\frac{1}{2}$, NE4, sec. 33, T31N, R57W, Sioux County, Nebraska). The stratotype section has been previously illustrated and described, and a paleomagnetic transect sampled (MacFadden and Hunt, 1998: 155, fig. 10). A composite stratigraphic section of the stratotype area that includes all lithofacies of the formation on both south and north walls of the Niobrara Canyon has also been published (Hunt, 1985: fig. 3; 1990: fig. 7).

The Geologic Names Committee of the U.S. Geological Survey has reserved the term Anderson Ranch Formation for the above-mentioned formation-rank lithostratigraphic unit (W.A. Bryant, written commun., May 22, 1995). Here it is my intent to replace the lithostratigraphic formation-rank term "Upper Harrison" beds used in this report with the new term Anderson Ranch Formation (see appendix).

BOUNDARIES: The lower contact of the formation in the type area and throughout Sioux County in northwestern Nebraska is a readily recognized erosional disconformity that has been mapped and illustrated in earlier publications (Hunt, 1978: fig. 17; 1985b: fig. 3; 1990: figs. 4, 7). The subjacent unit is almost invariably the Harrison Formation (Hatcher, 1902). However, the Upper Harrison beds are lithically distinct from the Harrison Formation, cannot be considered its upper part, and are separated from the Harrison beds by a regional unconformity. At Agate Fossil Beds National Monument a broad paleovalley has been incised into the Harrison Formation and filled by Anderson Ranch fluvial sediments that contain the celebrated Carnegie Hill mammalian bonebed (Hunt, 1990).

In much of Sioux County and in Niobrara and Goshen Counties in southeastern Wyoming, erosion has removed strata that may have once been present above the Anderson Ranch beds. However, in central Sioux County and in Platte County, Wyoming, younger Miocene units are disconformable on and locally incise the Anderson Ranch Formation.

An upper contact with younger beds does not occur in the type area at Niobrara Can-

yon or farther north in Sioux County where rocks above the Anderson Ranch Formation have been removed by erosion. However, to the southeast of the canyon on the divide between the Niobrara and White Rivers ($S\frac{1}{2}$, T30N, R55W and T29N, R55W), and along and to the south of the Niobrara River at Agate postoffice ($N\frac{1}{2}$ of T28N, R55W; $N\frac{1}{2}$, T28N, R56W), the Anderson Ranch Formation is disconformably overlain by the lowermost strata of the Runningwater Formation of Cook (1965). The lithostratigraphic relationship of the Anderson Ranch Formation and the lowermost Runningwater beds is particularly evident along the valley of the Niobrara River at Agate Fossil Beds National Monument where the contact between the two formations is well-exposed both north and south of the river. MacFadden and Hunt (1998: 157–159, fig. 14, Skavdahl Dam) published a reference section northeast of Agate postoffice showing the upper contact of the Anderson Ranch Formation (= Upper Harrison beds) with the Runningwater Formation.

The Anderson Ranch Formation in the Niobrara Canyon and to the north along the Pine Ridge in Sioux County conforms to Peterson's initial Upper Harrison concept. Unfortunately, Peterson (e.g., 1910: 263) also included in his Upper Harrison the lowermost Runningwater beds northeast of Agate on the Niobrara-White River divide and in the vicinity of Agate National Monument. Although the lower Runningwater beds appear similar in their pale orange-brown color to the Anderson Ranch Formation, on closer inspection the Runningwater strata contain on average a lesser percentage of volcanic glass shards, are distinguished by thin sheet-flood units interbedded with air-fall sediment, lack the siliceous paleosols of the Anderson Ranch, are invariably superposed on the older unit, and contain a younger mammalian fauna.

As suggested by the North American Stratigraphic Code (1983: 858), boundaries of lithostratigraphic units should be selected on the basis of lithologic properties that, where possible, coincide with the boundaries of genetic units. The lower and upper bounding contacts of the Anderson Ranch Formation in Sioux County, Nebraska, enclose a

lithofacies association defining a genetic rock unit (Hunt, 1990). Anderson Ranch outcrops in Niobrara, Goshen, and Platte Counties are in lateral continuity with those in Sioux County, demonstrating the regional extent of the formation from its type area in northwest Nebraska into southeastern Wyoming.

LITHIC CONTENT: The formation comprises characteristic lithofacies that are present throughout the type area in Nebraska and also occur in southeastern Wyoming. The principal lithofacies and their lithologic characteristics have been previously described (Hunt, 1985b: 164–177, figs. 4–11; 1990: 74–94, figs. 5–7). These include: (1) eolian volcanoclastic loess with siliceous paleosols; (2) lacustrine calcareous mudstone; (3) fluvial volcanoclastic sands and intraformational gravels; (4) calcareous tuff and fluvial silty sandstone accumulated in shallow waterholes.

Approximately 87% of outcrop of the formation is eolian volcanoclastic loess. Volcanic glass shards comprise 30–54% of the rock, and additional pyroclastic grains indicate a total pyrogenic fraction of 50–75%. The sediment is predominantly silty fine to very fine sandstone, massive, homogeneous in texture and fabric, and pale brown to light gray in color. This lithofacies includes numerous siliceous paleosols of great lateral extent, rich in dense, small diameter (0.5 mm) rhizolith networks, suggestive of grasslands (figs. 3, 4). These paleosols are characteristic of the formation and do not occur in the adjacent Harrison Formation, except for a siliceous paleosol developed on the terminal Harrison surface marking the initiation of the Anderson Ranch climatic regime.

Lacustrine calcareous mudstones constitute only about 2% of the formation but are conspicuously visible as widespread, thin, white micritic limestones that often are silicified. Calcareous mudstone grades laterally into fine volcanoclastic shoreline sands at the margins of these shallow lakes (fig. 5).

Fluvial cross- and horizontally stratified sandstones, siltstones, and intraformational gravels make up about 10% of formation outcrop, occupying broad shallow paleovalleys, local ephemeral channels, and tributary gullies. In Sioux County the sandstones are almost entirely made up of reworked, fine

volcanoclastic sand and silt; epiclastic debris is limited to rare, local lenses of arkosic sandstones derived from the Hartville Uplift to the west (fig. 22).

Waterholes that accumulated volcanic ash, limy mud, and fine volcanoclastic sand comprise a final lithofacies (fig. 5). These waterhole deposits are often the locus of major mammalian bonebeds. Diatomites also filled local ephemeral depressions within the paleovalleys.

MAPPABILITY AND THICKNESS: The formation was not mapped by Peterson and has not been mapped throughout its regional extent. A representative part of the type area in the Niobrara Canyon is mapped (Hunt, 1978: fig. 2, symbol Tm). The formation has also been mapped at Agate Fossil Beds National Monument where its lower and upper bounding contacts are well-defined (Hunt, 1984). The formation has also recently been mapped in the Spoon Butte and Lone Sand Hill 7.5-minute topographic quadrangles, along the Wyoming-Nebraska state boundary (R.M. Hunt, Open-File Maps, Nebraska Conservation and Survey Division).

The formation has been traced from the type section throughout Sioux County, Nebraska, demonstrated by a north-south profile from the Pine Ridge southward to Agate Fossil Beds National Monument (Hunt, 1978: fig. 17; 1985b: fig. 3; 1990, figs. 4, 7). Both south and north of the Niobrara Canyon in Sioux County the formation thins (Hunt, 1990, fig. 7), so that at Agate National Monument the thickest section is ~50 ft (15.2 m) and along the Pine Ridge north of the town of Harrison is ~55 ft (16.8 m). The type section is representative of the thickest exposures of the formation in Sioux County, which in the Niobrara Canyon attain a thickness of as much as 160 ft (~50 m).

The formation can be traced to the west into Niobrara County and southward to Goshen County where outcrop thickness is less than 200 ft (~60 m); however, over much of this area the unit continues into the subsurface and the lower contact is not exposed. The southernmost exposures of the formation in Platte County, Wyoming, near Wheatland and Chugwater, are of similar thickness and represent the youngest sediments attributed

to the Anderson Ranch Formation, identified by a latest Arikarean mammal fauna.

ABANDONMENT OF THE TERM "MARSLAND FORMATION": According to the North American Stratigraphic Code (1983, Article 20, p. 855), a formally defined unit may be abandoned due to "widespread misuse in diverse ways which compound confusion". Here I demonstrate a concern for nomenclatural stability should this term be retained, and recommend an alternative nomenclature to take its place as required by the Code.

The Marsland Formation was first proposed by Schultz (1938) who said it was "best exposed in Nebraska in the region about [the town of] Marsland along the Niobrara River where it includes some 150 feet of buff and gray, soft sandstones." No mapping, type section, or reference sections were presented. Later, a type section was indicated in an abstract (Schultz, 1941: secs. 23–27, T28N, R52W, and secs. 19 and 30, T28N, R51W) but was not described. The formation was first mapped by Lugn (1939: pl. 1), but in combination with another formation so that its geographic extent remained indeterminate. A type section or reference sections were not described nor were upper or lower bounding contacts explicitly designated. The formation was said to extend from Nebraska into Wyoming, Colorado, and South Dakota but no geographic determinants or lithologic descriptions were provided.

The Marsland Formation bears on the renaming of the Upper Harrison because Schultz (1941) explicitly stated that "In Nebraska and Wyoming, the Marsland [Formation] includes all the deposits formerly called 'Upper Harrison'." However, Lugn's (1939) map of the Marsland Formation (and the second unit, the Sheep Creek Formation, that was combined with it) does not include the type area of the Upper Harrison of Peterson (1909) nor most of its contiguous outcrop, thus inaugurating the confused usage of the term.

Shortly after the publications of Schultz and Lugn appeared, Cook and Gregory (1941) noted that it was unclear what was to be included in the Marsland Formation, and argued that the relationship of the Upper Harrison of Peterson to the Marsland was vague. Cook was aware that the "beds near

Marsland . . . are not the 'Upper Harrison' beds, but later and distinct from them" (Cook and Gregory, 1941: 549). He was the first to express what is believed today to be the actual relation of these units when he stated that: "The Marsland Formation as defined by Schultz includes . . . two separable formations, the 'Upper Harrison' beds and the [stratigraphically] higher, previously unnamed deposits exposed east of Marsland." Despite these statements, the lithic distinctions between these units remained unclear.

It was evident that Schultz's (1938) proposal to apply the term Marsland Formation as a replacement name for the Upper Harrison beds was inappropriate, for it failed to recognize that at least two distinct formation-rank units were included, and the type area of Peterson's Upper Harrison beds and most of its contiguous outcrop had been excluded. Although Cook and Gregory (1941: 549) had suggested that the term Marsland Formation be restricted to the rocks in the vicinity of Marsland, this usage was not accepted by Schultz and his associates who continued to apply the term to a much wider geographic area.

Eventually Cook (1960) began to apply a new formation-rank term, Runningwater Formation, to the beds in the vicinity of Marsland, while retaining the term "Upper Harrison" for the lower unit. However, Cook's death prevented an adequate definition of the Runningwater Formation. This was accomplished by McKenna (1965) who thoroughly reviewed the Marsland problem, and simultaneously published a posthumous manuscript by Cook (1965) that provided a type section, lithic description, and map of the type area of Cook's Runningwater Formation. Unfortunately, Cook (1965: 6) further complicated the issue when he suggested that the term Marsland not designate the beds in the vicinity of the town of Marsland but rather replace Peterson's term Upper Harrison, thus a proposal similar to Schultz's use of the term as a replacement name. McKenna (1965), Hunt (1978), and others followed this suggestion, designating two formation-rank units, a Marsland Formation (Peterson's Upper Harrison) overlain by Cook's Runningwater Formation. However, this amounted to a division of a unit (Marsland Formation of

Schultz) into subunits while using the name Marsland for one of the subdivisions, a practice discouraged by the North American Code (1983: Article 19g). The principal objection to this proposal that has emerged from recent study of these rocks is that no Upper Harrison beds occur in the immediate vicinity of Marsland or in the Marsland "type section" of Schultz (1941).

An alternative solution was proposed by Yatkola (1978) who mapped the rocks in the vicinity of Marsland that Schultz had regarded as the type area of his Marsland Formation. He continued the use of the term Marsland at the rank of formation to include all rocks between the Harrison Formation and Box Butte Formation in this area, and designated lower (unnamed) and upper (Runningwater) members. A type section of the unnamed lower member was measured in the same approximate location as our type section for the Anderson Ranch Formation, and it is evident that he intended his lower member to correspond to Peterson's Upper Harrison unit. Also, Yatkola (1978: 25) correctly recognized that reddish-brown sediments forming the Miocene outcrops northeast of Agate postoffice and continuing southward on the Niobrara-Whistle Creek divide that were considered Upper Harrison beds by Peterson (1910: 263) and Cook and Gregory (1941: 549) are in fact directly traceable into the Runningwater Formation. Although he noted that his lower member could not be mapped into the type area of Peterson's Upper Harrison beds, his lower and upper members closely correspond to the concept advocated here of two formation-rank units: Anderson Ranch Formation and Runningwater Formation.

It is evident that the term "Marsland Formation" has been applied at various times to almost all early Miocene formation-rank units within the area, both as separate entities and taken together. This degree of uncertainty and misuse would seem to satisfy the criterion stated in the Code as grounds for abandonment.

Accordingly, I employ the term Anderson Ranch Formation for the formation-rank unit defined in the Niobrara Canyon by Peterson (1909) as the Upper Harrison beds. Only rocks that can be traced outward from the

type area and section are to be included in the formation. In this area the Anderson Ranch Formation rests directly on the Harrison Formation. The formation-rank unit superposed on the Anderson Ranch Formation, most evident northeast of Agate postoffice and south of the Agate National Monument on the Niobrara-Whistle Creek divide, is the Runningwater Formation of Cook (1965). The term "Marsland Formation" is abandoned. As defined herein, the Anderson Ranch and Runningwater Formations are unconformity-bounded lithogenetic units of the type endorsed by the North American Stratigraphic Code (1983: Article 23d, e).

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APPENDIX

The John Anderson ranch, for which the formation is named, was one of the earliest cattle ranches in the vicinity of the Niobrara Canyon in Sioux County. When O.A. Peterson first explored the canyon in 1901, he made frequent references to the Andersons, occasionally lodged at the ranch, and repaired equipment there; his field outfit was cared for by them during the winter of 1901–1902 after his departure for the Carnegie Museum. Peterson's fieldnotes (Memorandum for Field Expedition, 1901, Section of Vertebrate Paleontology, Carnegie Museum of Natural History, Pittsburgh) document his work in the type area of the Upper Harrison beds along the south rim of

the canyon from August 10 to September 28, 1901, where he made a rich collection of oreodonts, horses, camels, and carnivores. In 1901 he considered these Niobrara Canyon outcrops the upper part of the Loup Fork beds, a term used by him as an equivalent of today's Arikaree Group. In 1904 he mistakenly applied the name "Nebraska beds" to the Upper Harrison unit, but later, realizing that this was in error, selected the term Upper Harrison beds for these fossiliferous deposits (Peterson, 1907, 1909a). The John Anderson ranch included the greater part of the Upper 33, one of the first large ranches in northwest Nebraska, originally owned by the cattleman Bartlett Richards from 1883 to 1897.

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